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The songs of the western European grasshoppers of the genus *Stenobothrus* in relation to their taxonomy (Orthoptera: Acrididae)

D. R. Ragge

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Synopsis

The male calling songs of nine species of the Gomphocerine genus *Stenobothrus* are described and fully illustrated with oscillograms at several different speeds. The courtship song is also described for the seven species in which such a song is known. The songs of three species (*festivus*, *bolivarii* and *apenninus*) are described for the first time. For each species a list is provided of references to any past published work on the songs, classified according to the kind of information given. Notes on recognition, using both morphology and song, are given for each species, and two identification keys are provided, one based mainly on morphology and the other on song. The value of the song as a taxonomic character is discussed.

Introduction

Stenobothrus is one of the better known genera of Gomphocerinae, a group that includes most of the common European grasshoppers of open grassland and moorland. They are well known for their characteristic songs and are widely used in bio-acoustic, ecological and cytogenetic research. The subfamily includes about 150 European species, of which over 20 are pests in parts of their range, seven of them being regarded as major ones (Tsyplenkov, 1970).

Stenobothrus is a widespread Palaearctic genus, including over 30 species living in habitats ranging from lush grassland to steppe and high mountains. Eleven species have been recorded from western Europe, of which three, *lineatus*, *nigromaculatus* and *fischeri*, become pests when they occur in sufficient numbers, causing damage to cereal grasses, hayfields and alfalfa (Bei-Bienko & Mishchenko, 1951; Tsyplenkov, 1970).

It is now well known that the songs of Gomphocerine grasshoppers are of great taxonomic value. Their role as a mate recognition system makes them particularly valuable in resolving

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complexes of sibling species and in establishing the status of local populations showing small morphological differences. There has so far been no comprehensive account of these songs, presented group by group and illustrated with oscillograms. The main aim of the present paper, and of similar papers already published (Ragge, 1986) or in preparation, is to provide such an account for the western European species, arranged systematically by group and fully illustrated with oscillograms at several different speeds.

No information has previously been published on the songs of three of the nine species included in this study (*festivus*, *bolivarii* and *apenninus*) and no oscillograms have previously been published for a further two (*fischeri* and *grammicus*). For the species in which published information on the song is already available, references to the sources are given, classified according to the kind of information published.

Acknowledgements

I am much indebted to Drs A. Gorochov and A. Kaltenbach, who have kindly lent me type-specimens or other material from their respective institutions. I should also like to thank Mr C. F. Dewhurst and Miss T. M. Howard, who kindly brought me live males of *S. stigmaticus* from the Isle of Man, and Mr E. C. M. Haes, who was kind enough to give me a live male of *S. rubicundulus* that he had collected in the Italian Alps.

I am particularly grateful to my colleague Mr W. J. Reynolds, who made the studio recordings used in this study, helped me in reviewing the past literature on the songs, tested the identification key based on morphological characters and provided valuable comments at various stages in the preparation of the paper.

Finally I wish to thank my wife, who has given me invaluable help in all my field-work.

Abbreviations of depositories

BMNH	British Museum (Natural History), London
MNCN	Museo Nacional de Ciencias Naturales, Madrid
NM	Naturhistorisches Museum, Vienna
ZI	Zoological Institute of the Academy of Sciences of the U.S.S.R., Leningrad

Methods

Recording and analysing the songs

All the field recordings of the songs used in this study were made in full sunshine (except recording 184/1 – see p. 405) using a Uher 4000, 4200 or 4200IC tape recorder and AKG D202 microphone; the tape speed was always 19 cm/s. The subjects were approached stealthily so that the microphone could be held (or rested on the ground) about 10 cm from them without causing any disturbance.

The studio recordings were made in the BMNH Acoustic Laboratory using a Kudelski Nagra IV tape recorder and Sennheiser MKH405 microphone or (recordings 119 and 121 only) Kudelski Nagra III tape recorder and AKG C61 microphone; the tape speed was 19 or 38 cm/s. In every case a bench lamp was used to provide light and radiant heat.

Further data are given in Tables 1 and 2 for the recordings used for the oscillograms reproduced in Figs 9–116. However, the song descriptions given for each species are in most cases based on many more recordings of numerous songs, all of which were analysed oscillographically. The oscillograms reproduced in the figures were chosen as being typical of the species concerned and, in some cases, showing the extent of intraspecific variation. Although I have given in Tables 1 and 2 the ambient air temperatures at the time of recording, it is really the body temperature of the singing insect that is important, and this is more dependent on radiant heat than on the air temperature; as the insects were always receiving radiant heat from the sun or a bench lamp, the conditions under which the recordings were made were more uniform than the different air temperatures might suggest.

All the oscillograms were made from recorded songs with a Mingograf 34T ink-jet recorder.

Table 1 Data for the field recordings of male songs of *Stenobothrus* used for oscillograms reproduced in this study. All these recordings were made from different males. Recordists' names are abbreviated as follows: DRR = D. R. Ragge; WJR = W. J. Reynolds.

Species	Locality	Date recorded and collected	Recordist	Shade air temperature	Recording No.
lineatus	FRANCE: Seine-Maritime, near Gamaches	11.viii.1983	DRR	24°C	511/2
	ITALY: Lazio, Monti Reatini, foot of chair-lift to Monte Terminilletto, 1700 m	11.ix.1985	DRR	18°C	608/4
nigromaculatus	FRANCE: Pyrénées-Orientales, near Saillagouse, Val d'Eyne	22.ix.1976	WJR	16°C	184/1
	FRANCE: Lozère, Causse Méjean, near Crosgarnon	31.vii.1982	DRR	16°C	482/2
	Same locality	31.vii.1982	DRR	16°C	482/3
	ITALY: Abruzzi, Gran Sasso d'Italia, Fossa di Paganica, 1680 m	31.viii.1985	DRR	23°C	603/4
	ITALY: Marches, Monti Sibillini, Forca di Presta, 1540 m	14.ix.1985	DRR	18°C	609/10
fischeri	FRANCE: Vaucluse, Mont Ventoux, road from Bédoin, 1350 m	15.viii.1977	DRR	23°C	237/1
	Same locality	15.viii.1977	DRR	23°C	237/3
	FRANCE: Alpes-Maritimes, near Col de Vence, 930 m	25.viii.1977	DRR	25°C	241/2
festivus	SPAIN: Madrid, near Guadarrama, Embalse de la Jarosa	19.vi.1984	DRR	22°C	531/6
grammicus	FRANCE: Vaucluse, Mont Ventoux, near Pavillon de Rolland, 800 m	11.viii.1977	DRR	23°C	233/4
	FRANCE: Vaucluse, Mont Ventoux, road from Bédoin, 1100 m	12.viii.1977	DRR	19°C	234/1
bolivarii	SPAIN: Madrid, near Navacerrada, Embalse de Navalmedio, 1300 m	26.vii.1983	DRR	26°C	501/8
stigmaticus	FRANCE: Haute-Vienne, near St Yrieix-la-Perche	30.viii.1978	WJR	21°C	268/2
	SPAIN: Madrid, near Navacerrada, Valle de Barranca	27.vii.1983	DRR	22°C	503/6

Table 1 – *cont.*

Species	Locality	Data recorded and collected	Recordist	Shade air temperature	Recording No.
apenninus	ITALY: Abruzzi, Gran Sasso d'Italia, Fossa di Paganica, 1680 m	31.viii.1985	DRR	24°C	603/2
	Same locality	31.viii.1985	DRR	19°C	603/3
	ITALY: Lazio, Monti Reatini, foot of chair-lift to Monte Terminilletto, 1700 m	11.ix.1985	DRR	18°C	608/1
rubicundulus	FRANCE: Alpes-Maritimes, near St Dalmas de Tende, La Minière de Vallaure, 1500 m	24.viii.1977	DRR	23°C	240/4
	ITALY: Trentino-Alto Adige, near Riva del Garda, Tremalzo, 1200 m	27.viii.1985	DRR	13°C	601/5

Table 2 Data for the studio recordings of male songs of *Stenobothrus* used for oscillograms reproduced in this study. All these recordings were made from different males except for 369 and 371, which were made on different days from the same male of *rubicundulus*. The recordist was W. J. Reynolds in every case.

Species	Locality	Date collected	Date recorded	Air temperature	Recording No.
lineatus	ENGLAND: Kent, near Wrotham, Trottiscliffe	10.viii.1978	11.viii.1978	25°C	260
	Same locality	12.viii.1978	13.viii.1978	29°C	321/1
	Same locality	12.viii.1978	13.viii.1978	28°C	322/2
nigromaculatus	FRANCE: Pyrénées-Orientales, near Saillagouse, Val d'Eyne	22.ix.1976	29.ix.1976	27°C	176
festivus	SPAIN: Madrid, near Guadarrama, Embalse de la Jarosa	19.vi.1984	4.vii.1984	—	527
stigmaticus	ISLE OF MAN: Langness Peninsula	1–6.viii.1974	8.viii.1974	24°C	119
	Same locality	1–6.viii.1974	9.viii.1974	24°C	121
	Same locality	30.viii.1983	6.ix.1983	23°C	497
rubicundulus	ITALY: Belluno, Pordoi Pass, below cable line to Pordoi Joch	4.ix.1980	16.ix.1980	26°C	369
	Same locality	4.ix.1980	18.ix.1980	25°C	371

Song terminology

The bio-acoustic terms used are defined as follows.

Calling song. The song produced by an isolated male.

Courtship song. The special song produced by a male when close to a female.

Syllable. The sound produced by one complete up and down movement of the hind legs (Fig. 1).

Echeme. A first-order assemblage of syllables (Fig. 1).

Echeme-sequence. A first-order assemblage of echemes (Fig. 1).

Momentary breaks in the sound (of at least 1·25 ms) during the course of a syllable are referred to as 'gaps' (Fig. 1).

Presentation

The presentation is identical to that used in my recent paper on *Omocestus* Bolívar (Ragge, 1986: 215–219). As in that study I have relied mainly on oscillograms in presenting information on the songs and have kept the verbal descriptions as brief as possible. The references to past accounts of the songs are not exhaustive but are intended to include all sources that the reader might find useful to refer to for additional or confirmatory information.

The speeds of the oscillograms are (after reduction for printing) 10 mm/s, 80 mm/s, 320 mm/s and 1280 mm/s, although the higher speeds are given only when considered to be useful. For three species (*lineatus*, *festivus* and *stigmaticus*) I have included oscillograms taken from the calling songs of males with only one hind leg; such oscillograms, at the higher speeds, show the individual peg-impacts with particular clarity (see Figs 30, 61, 93).

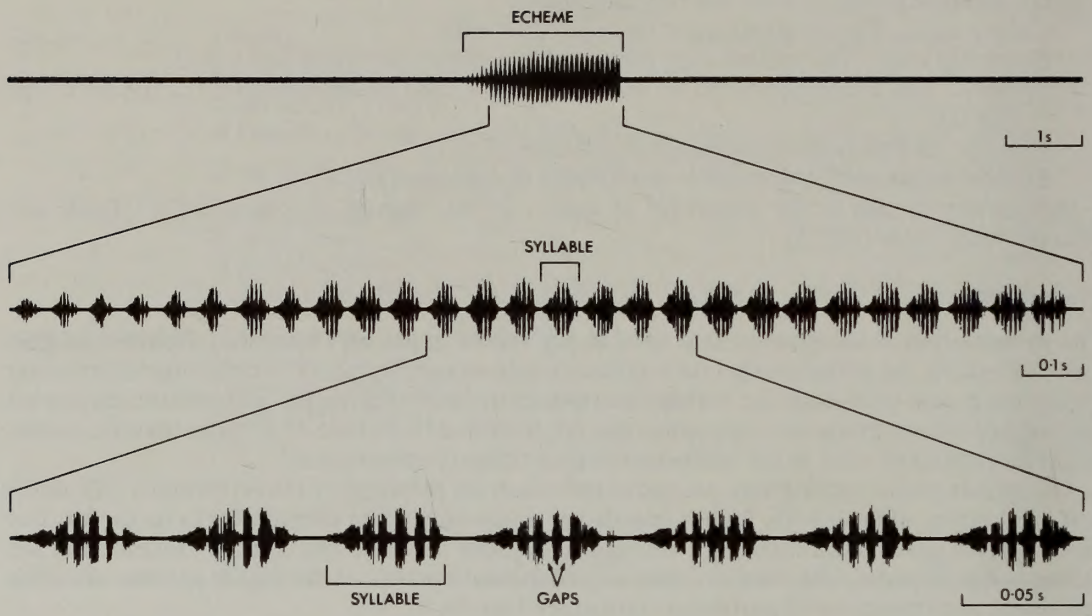
The song as a taxonomic character

In my paper on *Omocestus* I outlined the history of the use of the songs of Orthoptera in taxonomy (Ragge, 1986: 219–220) and more recently (Ragge, in press) I have emphasized the particular importance of the songs in the taxonomy and biogeography of several groups of western European Orthoptera. The taxonomic value of the male calling songs of the western European species of *Stenobothrus* can be seen at a glance from Figs 9–17. The song-patterns show a wide variety from the long single echeme of *lineatus*, lasting more than 10 s and with a syllable repetition rate of less than 2/s, to the rapid series of short echemes of *grammicus* and *bolivarii*, in which each echeme lasts less than 0·2 s and the syllable repetition rate is more than 50/s.

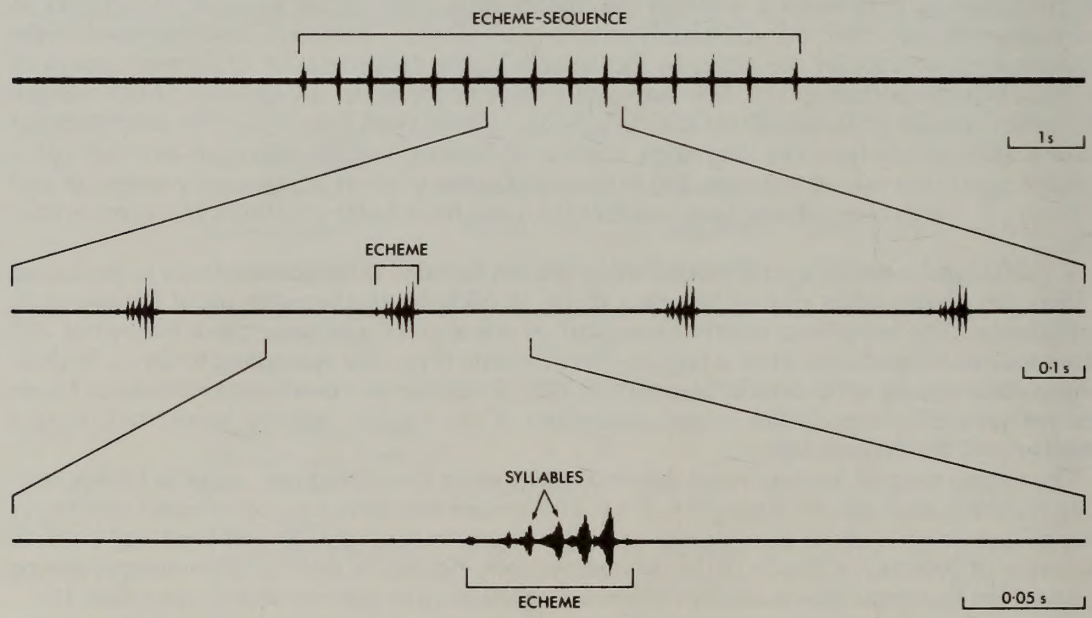
S. rubicundulus stands apart from the other species included in the present study in producing a loud wing-buzz, often during hovering flight, in addition to the more usual femoro-alary stridulation. The wing-buzz clearly forms part of this species' communicative behaviour and often follows immediately after a femoro-alary echeme (Fig. 17). According to Dr C. Walter, whose observations are quoted by Harz (1975: 777), *S. cotticus* also produces a wing-buzz; I have not yet been able to study the acoustic behaviour of this species, which is known only from a small area of the French Alps.

The calling song of *lineatus* is unique among all known Gomphocerine songs in having such long syllables, each usually lasting 0·6–0·8 s. This species also has a uniquely dense stridulatory file, so that, in spite of the slow leg movements, the peg-impact rate (for *one* hind leg) is still of the order of 500/s in the middle of the downstroke (see Fig. 30). *S. lineatus* is also unique among the western European species of *Stenobothrus* in producing an echeme lasting more than 10 s.

Among the other species in which the calling song normally consists of a single echeme (*fischeri*, *festivus*, *stigmaticus* and *apenninus*), the song conforms to the same basic pattern of a simple series of syllables, beginning quietly but soon reaching maximum intensity (see Figs 11, 12, 15, 16). The number and repetition rate of the syllables enable *fischeri* and *festivus* to be distinguished from the other two species and also from each other. However, *stigmaticus* and *apenninus* are extremely similar to each other in both calling and courtship songs; although the echemes of *stigmaticus* are on average longer than those of *apenninus* and are composed of more



Stenobothrus stigmaticus



Stenobothrus grammicus

Fig 1 Oscillograms of the male calling songs of two species of *Stenobothrus*, showing the terminology used in this paper.

syllables, there is an overlap in both these song characters and I have not been able to find a constant difference between the two songs. As these two species are completely allopatric I think it likely that *apenninus* is a recent derivative from *stigmaticus* that has diverged from it morphologically as a result of isolation in the Apennine mountain range. It would be most interesting to establish experimentally whether there is any ethological barrier to intercopulation between these two species.

The remaining three species, *nigromaculatus*, *grammicus* and *bolivarii*, have calling songs consisting of a sequence of echemes; they also differ from the other six species in having syllable repetition rates of more than 50/s. As can be seen from Figs 10, 13 and 14, the calling song of *nigromaculatus* differs markedly from those of *grammicus* and *bolivarii* in that the constituent echemes are far fewer in number (usually 2–6) and much longer (usually lasting 1–2 s). The very short, rapidly repeated echemes of *grammicus* and *bolivarii* show a marked contrast with the other seven species, but sound similar to each other to the unaided ear, differing mainly in the syllable structure within the echemes. These two species are also similar morphologically and may well have evolved from common stock quite recently.

As I have recently emphasized (Ragge, 1986: 220), the value of the songs as indicators of phylogeny is very limited. Their taxonomic importance, as would be expected of a mate recognition system, is almost entirely at the specific and subspecific levels. This can be exemplified by some fairly close intergeneric resemblances in song between certain species of *Stenobothrus* and *Omocestus*. The male calling song of *S. apenninus*, for example, is quite similar to that of *O. raymondi* (Yersin) (Ragge, 1986: figs 64–72), and there is also quite a close resemblance between the male calling songs of *S. fischeri* and *O. broelemanni* (Azam) (Ragge, 1986: figs 90–98). The members of each of these pairs are allopatric and so they have no need for differing recognition signals (although in each case there is a marked difference in *courtship* song). The calling song of all four of these species is a simple echeme and has presumably not been subject to the selective pressures needed for further differentiation. Echemes of this basic type also occur in several species of *Chorthippus* Fieber.

New lectotype designations

Gomphocerus (Stenobothrus) Bolivarii Brunner, *in* Bolívar, 1876: 327.

Dr A. Kaltenbach of the NM, Vienna has kindly sent me a number of syntypes of this species, and I have selected and labelled a male as lectotype. I have labelled two other males and six females as paralectotypes.

Stenobothrus apenninus Ebner, 1915: 551.

Dr Kaltenbach has also kindly lent me six syntypes of this species, and I have selected and labelled an adult male as lectotype; this specimen was already labelled 'typus' by Ebner. I have labelled the remaining five specimens (two adult males, one adult female and two female nymphs, all labelled 'paratypus') as paralectotypes.

STENOBOTHRUS Fischer

Stenobothrus Fischer, 1853: 313. Type-species: *Gryllus lineatus* Panzer, by subsequent designation (Kirby, 1910: 160).

Stenobothrodes Tarbinskii, 1948: 116 [as subgenus of *Stenobothrus* Fischer]. Type-species: *Stenobothrus eurasius* Zubovskii, by monotypy. **Syn. n.**

Crotalacris Chopard, 1952: 280 [as subgenus of *Stenobothrus* Fisher]. Type-species: '*Stenobothrus rubicundus* (Germar)' [= *Stenobothrus rubicundulus* Kruseman & Jeekel (see p. 422)], by monotypy. [Synonymized with *Stenobothrodes* Tarbinskii by La Greca, 1965: 70.]

Diagnosis. ♂♀. Head of typical Gomphocerine shape, foveolae well developed. Antennae usually filiform or slightly thickened towards tip, exceptionally clubbed (males of *S. clavatus* Willemse). Pronotal lateral carinae varying from sharply incurved to almost straight. Brachypterous to macropterous. Fore wings without bulge on anterior margin of precostal area; medial area usually widened, often conspicuously so, with Cu_1 and Cu_2 sometimes partly or even completely fused. Hind wings varying from transparent to strongly smoky, sometimes with enlarged medial area. Ovipositor with lateral tooth on each valve. Tympanal aperture slit-like.

DISCUSSION. *Stenobothrus* can be recognized reliably only by the ovipositor, which has a lateral tooth on all four valves. Males can sometimes be confused with *Omocestus*, but in most cases can be recognized by the widened medial area of the fore wings. Both sexes of most species have somewhat broader pale bands along the pronotal lateral carinae than are shown by *Omocestus* and other related genera.

The subgenera *Stenobothrodes* and *Crotalacris* are certainly not distinct from each other at the subgeneric level, and even considered together they do not in my opinion justify recognition as a distinct subgenus. On the other hand, I have followed Harz (1975) and other recent workers on the European fauna in regarding *Omocestus* and *Myrmeleotettix* Bolívar as distinct genera rather than subgenera of *Stenobothrus*; *Stauroderus* Bolívar and the Nearctic genus *Bruneria* McNeill, neither of which has a toothed ovipositor, are similarly excluded.

As in the other large Gomphocerine genera *Omocestus* and *Chorthippus*, the male calling songs show a wide range of patterns in *Stenobothrus*, varying from the long single echeme of *lineatus* to the rapid sequence of short echemes of *grammicus* and *bolivarii*, and the remarkable wing-buzz of *rubicundulus*.

DISTRIBUTION. All Europe, the larger Mediterranean islands, North Africa and temperate Asia as far as Mongolia.

INCLUDED SPECIES. *S. amoenus* (Brisout), *S. apenninus* Ebner, *S. berberus* Uvarov, *S. bolivarii* (Brunner), *S. bulgaricus* Ramme, *S. burri* Karabag, *S. carbonarius* (Eversmann), *S. caucasicus* Dovnar-Zapolskii, *S. clavatus* Willemse, *S. cobresianus* Bei-Bienko, *S. cotticus* Kruseman & Jeekel, *S. crassipes* (Charpentier), *S. croaticus* Ramme, *S. eurasius* Zubovskii, *S. festivus* Bolívar, *S. fischeri* (Eversmann), *S. graecus* Ramme, *S. grammicus* Cazurro, *S. kirgizorum* Ikonnikov, *S. lineatus* (Panzer), *S. maroccanus* Uvarov, *S. miramae* Dirsh, *S. newskii* Zubovskii, *S. nigromaculatus* (Herrich-Schäffer), *S. palpalis* Uvarov, *S. posthumus* Ramme, *S. rubicundulus* Kruseman & Jeekel, *S. stigmaticus* (Rambur), *S. sviridenkoi* Ramme, *S. tadzhicus* Mishchenko, *S. ursulae* Nadig, *S. werneri* Adelung, *S. zubowskyi* Bolívar.

Keys to the principal western European species of *Stenobothrus*

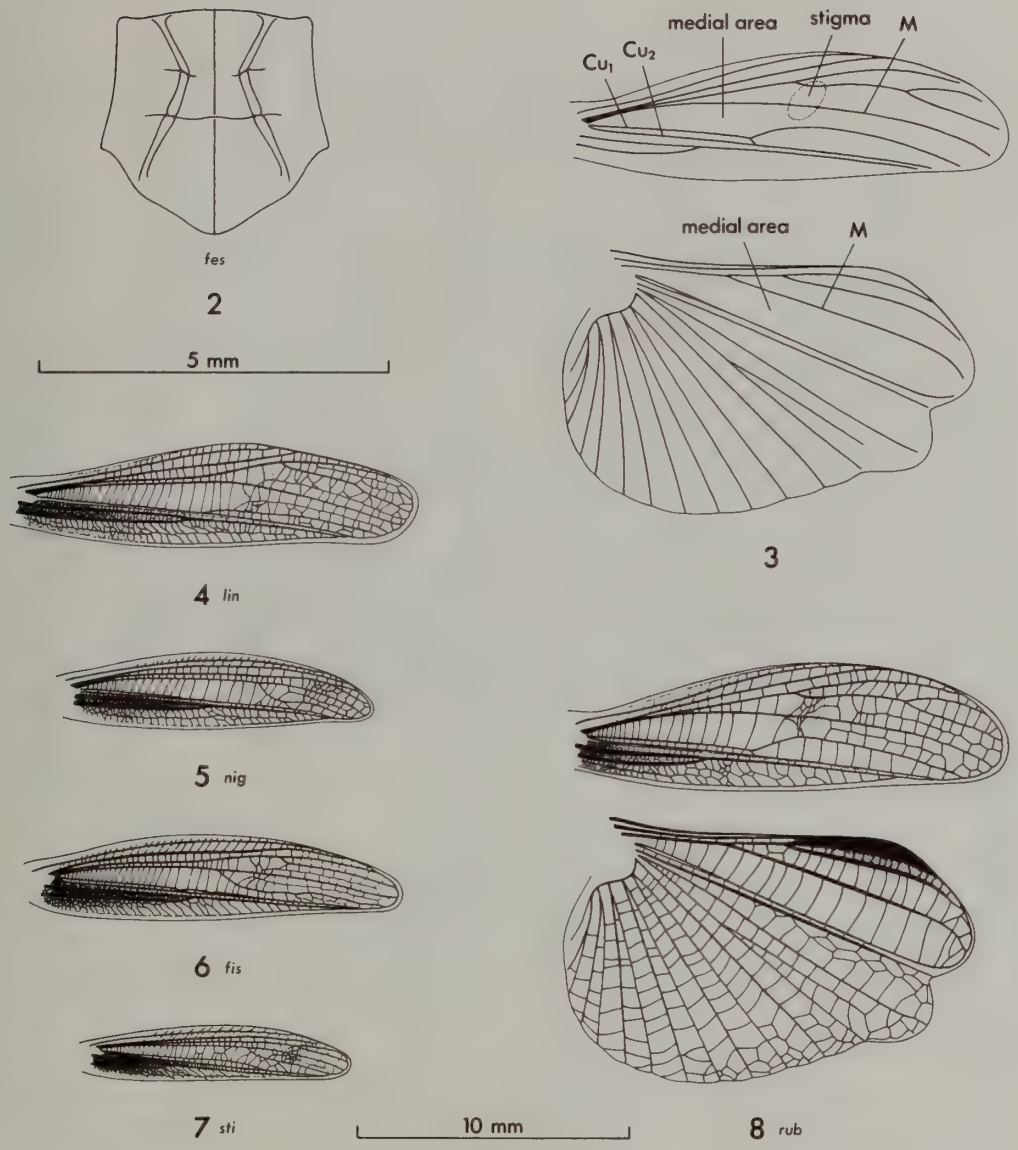
The only western European species not included in these keys are very local forms, sometimes of doubtful status, in which the song is unknown to me.

Two keys are provided here, one based on morphological characters but with notes on song differences added where appropriate, and one based entirely on the male calling songs. Some of the species are difficult to separate morphologically and, in the absence of song information, some specimens may not be correctly identified using the morphological key. Reference should in any case always be made to the notes given on recognition in the accounts of each species.

Key based primarily on morphological characters

This key is for sexually mature adults, either freshly collected or showing good colour preservation. The terminology used for wing characters is illustrated in Fig. 3.

1 Hind wings vestigial in both sexes; fore wings reduced to about the same length as the pronotum in ♀ (Apennine mountains) ..... ***apenninus*** (p. 418)
– Both pairs of wings well developed 2
2 Palps black or dark brown at the tip ..... ***grammicus*** (p. 410)
– Palps not black or dark brown at the tip 3
3 Male 4
– Female 10
4 Last segment of the maxillary palps bulbous and usually coloured orange-pink, red-brown or yellow brown ..... ***bolivarii*** (p. 413)
– Last segment of the maxillary palps not bulbous and not coloured pink or brown 5
5 Pronotal lateral carinae clearly angled in the prozona and interrupted at the angle by an additional transverse sulcus (Fig. 2) ..... ***festivus*** (p. 410)
– Pronotal lateral carinae not or hardly angled in the prozona and not interrupted by an additional sulcus (not as in Fig. 2) 6
6 Stigma within 3 mm of the fore wing-tip 7
– Stigma further than 3 mm from the fore wing-tip 8
7 Medial area of the fore wing enlarged, as in Fig. 5, Cu_1 becoming fused with Cu_2 within the proximal half of the fore wing. Total length more than 14 mm. (Song a sequence of two or more echemes, as in Figs 31–34) ..... ***nigromaculatus*** (p. 405)



Figs 2–8 Pronotum and wings of species of *Stenobothrus*. 2. Dorsal view of the pronotum of *S. festivus*. 3. The right male fore and hind wings of *S. rubicundulus*, showing the principal veins and the wing terminology used in this paper. 4–7. The right male fore wing of (4) *S. lineatus*, (5) *S. nigromaculatus*, (6) *S. fischeri*, (7) *S. stigmaticus*. 8. The right male fore and hind wings of *S. rubicundulus*.

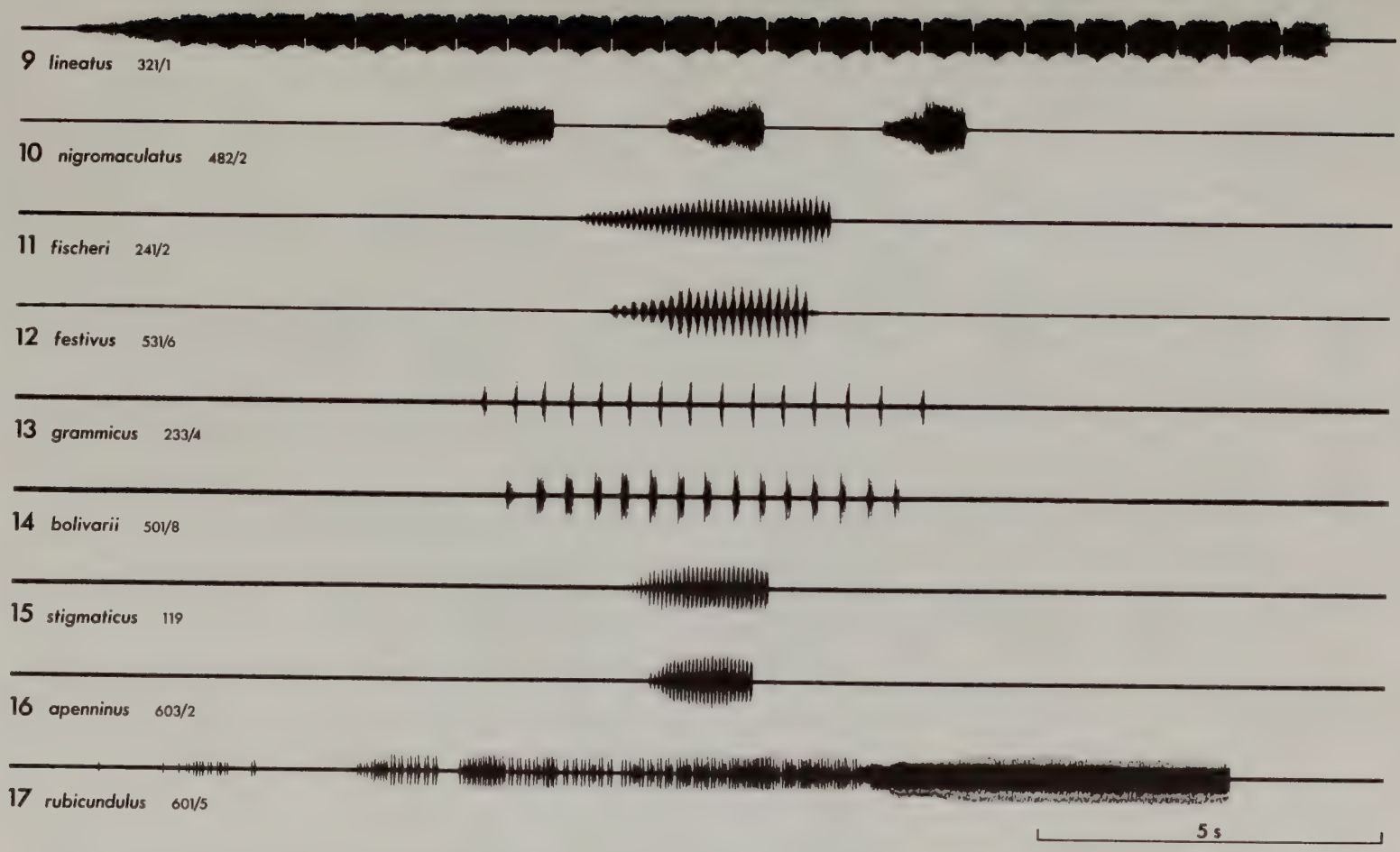
– Medial area of the fore wing not enlarged, as in Fig. 7, Cu_1 remaining separate from Cu_2 until the distal half of the fore wing. Total length less than 14 mm. (Song almost always a single echeme, as in Fig. 15) ..... ***stigmaticus*** (p. 413)
8 Cu_1 fused with Cu_2 at or near the base of the fore wing, as in Fig. 4. Cerci conical. (Song with syllable repetition rate less than 2/s) ..... ***lineatus*** (p. 404)
– Cu_1 remaining distinct from Cu_2 in much of the proximal half of the fore wing (although the two veins often touch in places), not as in Fig. 4. Cerci laterally compressed towards the tip. (Song with syllable repetition rate more that 4/s) 9
9 Fore wings very broad, as in Fig. 8. Hind wings as in Fig. 8, with the more distal part of the anterior margin strongly sclerotized and a much enlarged medial area ..... ***rubicundulus*** (p. 422)
– Fore wings much narrower, as in Fig. 6. Hind wings not as in Fig. 8 ..... ***fischeri*** (p. 405)
10 Cu_1 fused or continguous with Cu_2 in at least part of the proximal half of the fore wing 11
– Cu_1 remaining separate from Cu_2 until the distal half of the fore wing 14
11 Stigma within 4 mm of the fore wing-tip ..... ***nigromaculatus*** (p. 405)
– Stigma further than 4 mm from the fore wing-tip 12
12 Cu_1 fused with Cu_2 at or near the base of the fore wing ..... ***lineatus*** (p. 404)
– Cu_1 remaining distinct from Cu_2 in much of the proximal half of the fore wing (although the two veins sometimes touch or fuse in places) 13
13 Hind wings as in Fig. 8, with the more distal part of the anterior margin strongly sclerotized and a much enlarged medial area ..... ***rubicundulus*** (p. 422)
– Hind wings not as in Fig. 8 ..... ***fischeri*** (p. 405)
14 Length of the fore wings less than 11 mm ..... ***stigmaticus*** (p. 413)
– Length of the fore wings more than 11 mm 15
15 Hind wings as in Fig. 8, with the more distal part of the anterior margin strongly sclerotized and a much enlarged medial area ..... ***rubicundulus*** (p. 422)
– Hind wings not as in Fig. 8 16
16 Length of the fore wings more than 15 mm ..... ***bolivarii*** (p. 413)
– Length of the fore wings less than 15 mm 17
17 Pronotal lateral carinae clearly angled in the prozona and interrupted at the angle by an additional transverse sulcus (Fig. 2). Cu_1 and Cu_2 diverging in the proximal half of the fore wings ..... ***festivus*** (p. 410)
– Pronotal lateral carinae not or hardly angled in the prozona and not normally interrupted by an additional sulcus (not as in Fig. 2). Cu_1 and Cu_2 converging or running parallel in the proximal half of the fore wing 18
18 Stigma within 4 mm of the fore wing-tip ..... ***nigromaculatus*** (p. 405)
– Stigma further than 4 mm from the fore wing-tip ..... ***fischeri*** (p. 405)

Key based on song characters (see especially Figs 9–17)

This key is based on the calling songs produced by isolated males in warm, sunny conditions. Many of the song differences can be easily detected by the human ear assisted by the second hand (or digital count) of a watch, but a few of the couplets require oscillographic analysis, or at least the ability to play back the recorded song at a slower tape speed. I have been unable to find a consistent difference between the calling songs of *stigmaticus* and *apenninus* (couplet 9), but these species are completely allopatric and easily separated morphologically.

See p. 397 for definitions of the terms 'echeme', 'syllable' and 'gap'.

1 Song consisting, at least partly, of a loud buzz produced by wing-vibration, either on the ground or in flight (Figs 109–116) ..... ***rubicundulus*** (p. 422)
– Song produced entirely by femoro-alary stridulation 2
2 Song a sequence of echemes in rapid succession (at least 1/s) 3
– Song a single echeme or a sequence of echemes repeated at the rate of one every 2 s or more slowly 4
3 Each echeme lasting less than 80 ms, loudest towards the end (Figs 62–72) ..... ***grammicus*** (p. 410)
– Each echeme lasting more than 80 ms, loudest at the beginning (Figs 73–76) ..... ***bolivarii*** (p. 413)
4 Song consisting of a single echeme lasting more than 10 s and produced by very slow leg movements (less than 2/s); syllables lasting 0·5–1·0 s (Figs 18–30) ..... ***lineatus*** (p. 404)
– Song consisting of one or more echemes, each lasting less than 10 s and produced by more rapid leg movements (at least 3/s); syllables lasting less than 0·2 s 5
5 Echeme usually lasting more than 5 s, with the syllables, at least in the early part of the echeme,



Figs 9–17 Oscillograms of typical male calling songs of species of *Stenobothrus*. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 395, 396).

composed of clearly separated upstroke and downstroke sounds of equal amplitude, as in Figs 103–108 ..... ***rubicundulus*** (p. 422)
– Echeme lasting less than 5 s, with the syllables composed mainly of downstroke sounds (not as in Figs 103–108) 6
6 Song consisting of at least 2 echemes; syllable repetition rate more than 50/s (Figs 31–44) ***nigromaculatus*** (p. 405)
– Song almost always consisting of a single echeme; syllable repetition rate less than 20/s 7
7 Echeme composed of more than 40 syllables and usually lasting more than 3 s (Figs 45–53) ***fischeri*** (p. 405)
– Echeme composed of fewer than 40 syllables and usually lasting less than 3 s 8
8 Syllable repetition rate less than 12/s; early part of echeme with about 7–8 gaps in each syllable (Figs 54–61) ..... ***festivus*** (p. 410)
– Syllable repetition rate usually more than 12/s; early part of echeme with fewer than 5 gaps in each syllable (Figs 77–102) 9
9 Occurring only in the Apennine mountains ..... ***apenninus*** (p. 418)
– Not occurring in the Apennine mountains ..... ***stigmaticus*** (p. 413)

The songs of the western European *Stenobothrus*

Stenobothrus lineatus (Panzer)

(Figs 4, 18–30)

Gryllus lineatus Panzer, 1796: 9. Type(s): GERMANY (lost); the two 'neotypes' designated by Harz (1975: 759) are clearly invalid.

REFERENCES TO SONG. **Oscillogram**: Dumortier, 1963; Elsner, 1974*a*, 1975; Elsner & Popov, 1978; Grein, 1984; Haskell, 1957, 1958. **Diagram**: Bellmann, 1985*a*; Duijm & Kruseman, 1983; Haskell, 1957; Jacobs, 1950, 1953; Luquet, 1978; Ragge, 1965. **Frequency information**: Dumortier, 1963; Haskell, 1957, 1958. **Musical notation**: Yersin, 1854. **Verbal description only**: Baier, 1930; Broughton, 1972; Chopard, 1922, 1952; Faber, 1928, 1953; Harz, 1957; Haskell, 1955. **Disc recording**: Andrieu & Dumortier, 1963; Grein, 1984; Ragge, Burton & Wade, 1965. **Cassette recording**: Bellmann, 1985*b*.

RECOGNITION. Males of this species may be distinguished from the rather similar species *nigromaculatus* and *fischeri* by the cerci, which are simply conical (laterally compressed towards the tip in the other two species). In both sexes the veins Cu_1 and Cu_2 are more completely fused together in the fore wings than in *nigromaculatus* and *fischeri*, and the hind wings are more strongly smoky.

In the field males may be recognized at once by their highly characteristic calling song, in which the syllable repetition rate (under 2/s) is lower than in any other European grasshopper.

SONG (Figs 18–30). The calling song of this species is unique among the western European Gomphocerinae in both the slowness of the leg movements and the quality of the sound produced. It consists of an echeme lasting about 10–25 s and composed of about 15–35 syllables repeated at the rate of about 1·2–1·5/s. The echeme usually begins quietly but reaches maximum intensity within a few syllables. The sound is usually continuous, with a highly characteristic, rather wheezy quality, and showing slight fluctuations in intensity corresponding with the leg movements – though partly masked by the fact that one hind leg always moves slightly in advance of the other.

In the presence of a female the male usually produces longer echemes (with a more gradual crescendo at the beginning), sometimes lasting a minute or more but otherwise similar to the calling song. Between these echemes the male produces a quite different 'ticking' sound (Figs 21, 22, 26, 27) by moving the hind legs through a much smaller angle than in the calling song and at a much higher rate (usually 5–7 syllables/s). This ticking sound lasts typically for about half a minute before another echeme of the calling song type is produced, but it may be greatly prolonged, sometimes lasting for even longer than an hour. The ticking sound and the 'calling song' echemes usually alternate several times before the male attempts to copulate with the female. The courtship song of this species and the leg movements that produce it have been described in great detail by Elsner (1974*a*, 1975).

DISTRIBUTION. Widespread in Europe, but not reaching further north than southern Sweden and limited to mountains in the southern peninsulas. The range extends eastwards across central Asia to Mongolia.

Stenobothrus nigromaculatus (Herrich-Schäffer)

(Figs 5, 31–44)

Acridium nigromaculatum Herrich-Schäffer, 1840: 10. Type(s) unknown; the two 'neotypes' designated by Harz (1975: 761) are clearly invalid.

REFERENCES TO SONG. **Oscillogram**: Grein, 1984; Schmidt & Schach, 1978. **Diagram**: Bellmann, 1985*a*; Duijm & Kruseman, 1983; Jacobs, 1950, 1953. **Verbal description only**: Faber, 1928, 1953; Harz, 1957. **Disc recording**: Grein, 1984. **Cassette recording**: Bellmann, 1985*b*.

RECOGNITION. Males of this species may be distinguished from *lineatus* by the cerci, which are laterally compressed towards the tip (simply conical in *lineatus*). In the fore wings of both sexes the veins Cu_1 and Cu_2 are less completely fused together than in *lineatus*, and the stigma is nearer the wing-tip than in *fischeri* (cf. Figs 5, 6).

In the field males may be recognized quite easily by their calling song, in which the syllable repetition rate (about 70–110/s) is much higher than in *lineatus* (about 1·2–1·5/s) and *fischeri* (about 10–15/s).

SONG (Figs 31–44). The calling song consists of a series of 2–6 echemes (each beginning quietly but showing a rapid crescendo), separated by intervals of 1–3 s. Each echeme lasts about 0·8–2·0 s (rarely up to 2·5 s) and consists of about 90–200 syllables (rarely up to 250) repeated at the rate of about 70–110/s.

In the presence of a female the male produces a quite complicated courtship song, consisting of two alternating phases (Figs 35, 36, 41–44). The first phase consists of a series of fairly quiet echemes separated by intervals of about 0·6–0·9 s; during these intervals a few even quieter sounds are often produced. Each echeme lasts for about 0·3–0·9 s and is composed of about 40–80 syllables repeated at the rate of about 80–100/s. This phase lasts for an indefinite period, usually more than 30 s and often several minutes. The second phase, which follows abruptly, consists of a series of about 3–7 louder and longer echemes, each of which is preceded by a much shorter echeme. The shorter echemes last for less than half a second, and in fact after the first longer echeme they are often reduced to little more than a single syllable. The longer echemes usually last for about 0·8–2·2 s and are subdivided into two parts, one with slower syllables (about 40–60/s) and one with faster syllables (about 70–120/s). At the end of this second phase the male either attempts to copulate with the female or, after a short pause, begins the first phase again.

Note that the difference in temporal pattern between the oscillograms taken from recording 482/3 (Figs 35, 41, 42) and those taken from recording 184/1 (Figs 36, 43, 44) may have been caused, at least partly, by the fact that recording 184/1, unlike any other field recording used in this study, was made in conditions of hazy sunshine, so that the subject was receiving less radiant heat than it would have in full sunshine.

DISTRIBUTION. Southern Europe and central Asia; absent from the Iberian Peninsula except in the vicinity of the Pyrenees, and confined to uplands in the Italian and Balkan Peninsulas.

Stenobothrus fischeri (Eversmann)

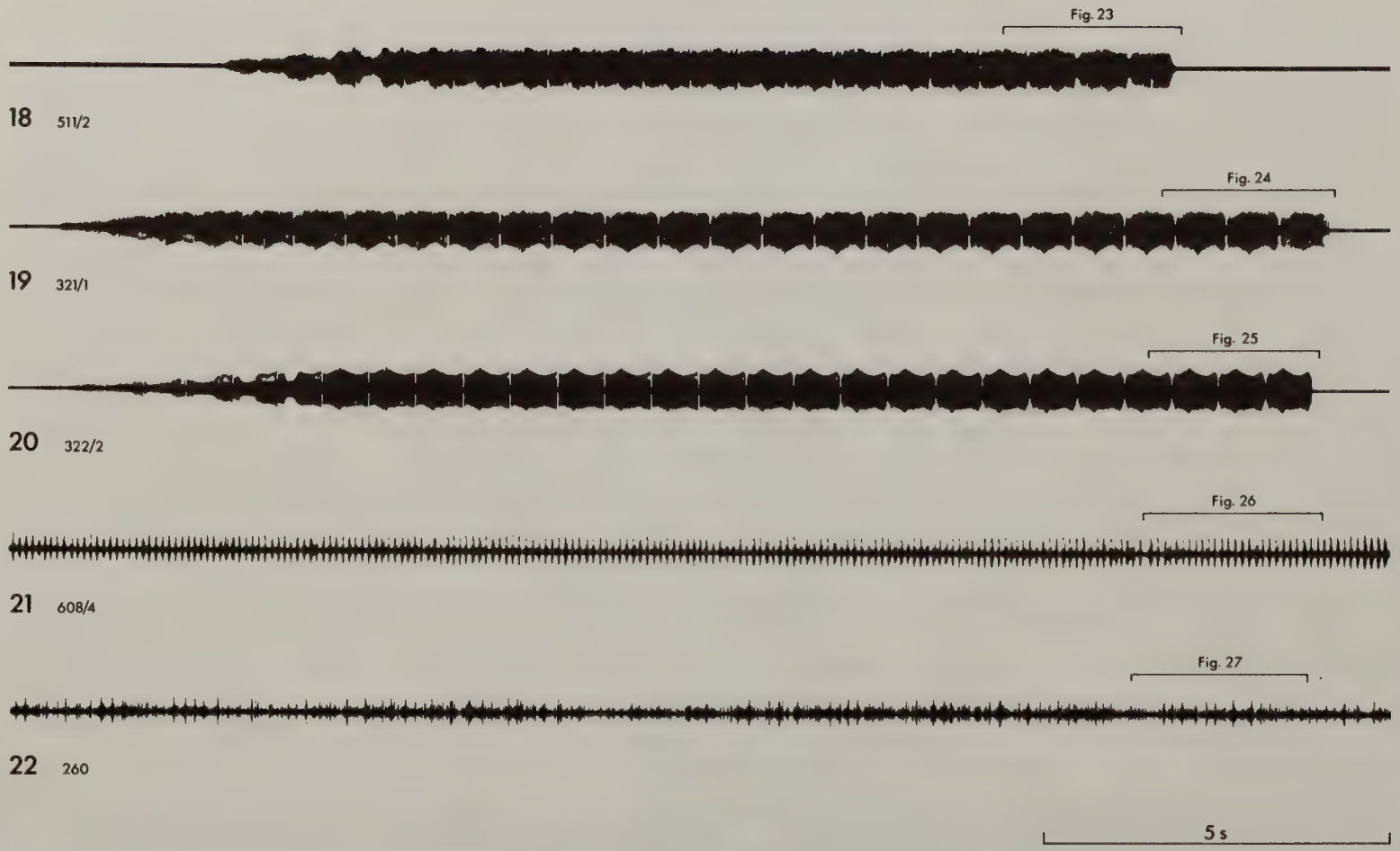
(Figs 6, 45–53)

Oedipoda fischeri Eversmann, 1848: 11. Syntypes of both sexes, U.S.S.R.: Ural Mountains (ZI, Leningrad) [1 ♂, 1 ♀ syntypes examined].

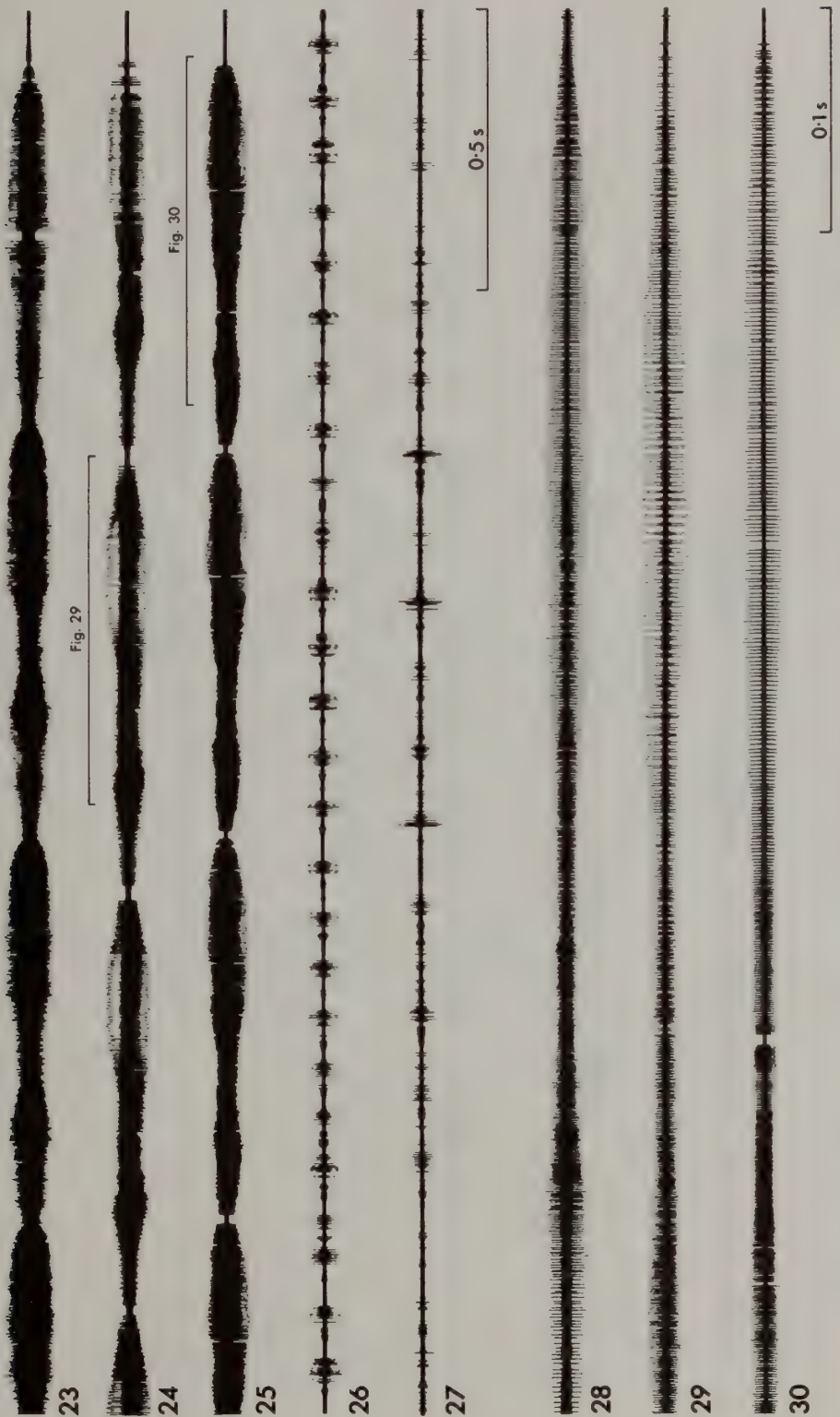
REFERENCES TO SONG. **Diagram**: Luquet, 1978. **Verbal description only**: Faber, 1953; Harz, 1957.

RECOGNITION. Males of this species may be distinguished from *lineatus* by the cerci, which are laterally compressed towards the tip (simply conical in *lineatus*). In the fore wings of both sexes the veins Cu_1 and Cu_2 are less completely fused together than in *lineatus* and the stigma is further from the wing-tip than in *nigromaculatus* (cf. Figs 5, 6).

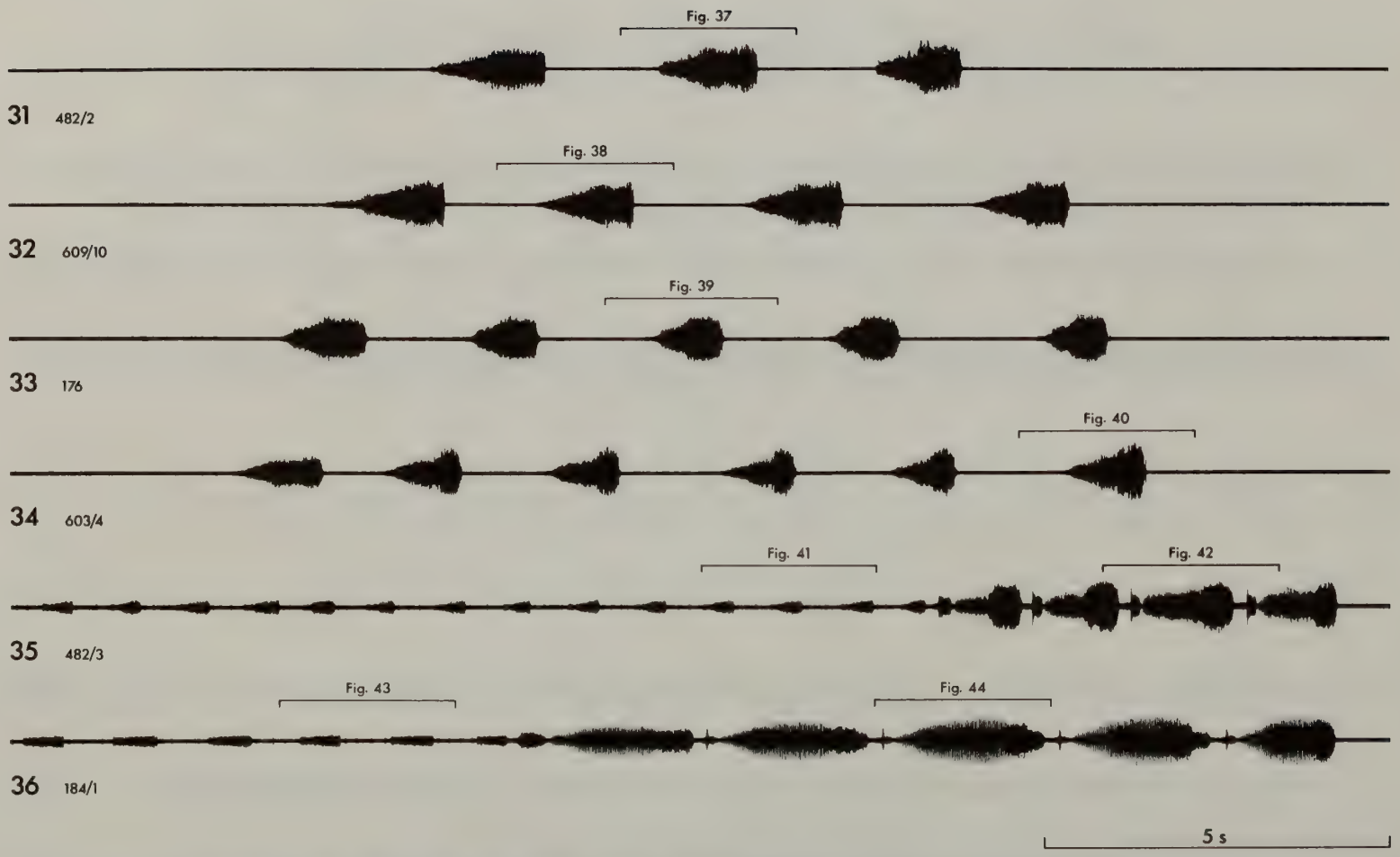
In the field the single echeme of the male calling song, which lasts for 3–5 s and is composed of more than 40 syllables, enables this species to be distinguished from *lineatus*, *nigromaculatus*, *grammicus* and *bolivarii*. The calling songs of *festivus* and *stigmaticus* are more similar, but in both these species the echeme is shorter, with fewer than 40 syllables.



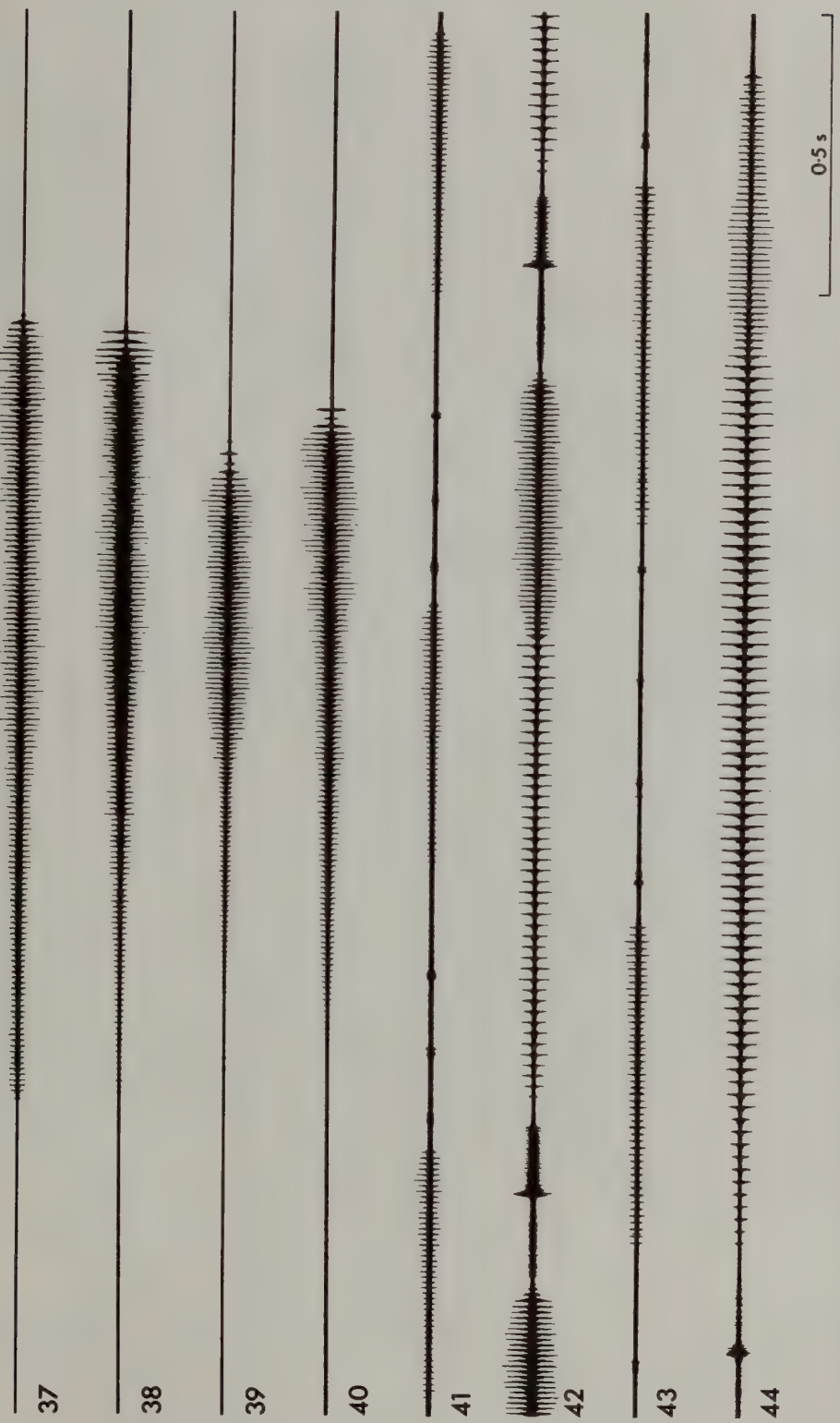
Figs 18–22 Oscillograms of the songs of five males of *Stenobothrus lineatus*. 18–20. Calling songs of males with (18, 19) two hind legs and (20) one hind leg. 21, 22. Part of two courtship songs. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 395, 396).



Figs 23–30 Faster oscillograms of the indicated parts of the songs of *Stenobothrus lineatus* shown in Figs 18–22. Figs 25 and 30 are from a male with only one hind leg.



Figs 31–36 Oscillograms of the songs of six males of *Stenobothrus nigromaculatus*. 31–34. Calling songs. 35, 36. Part of two courtship songs (see the remarks on p. 405). The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 395, 396).



Figs 37–44 Faster oscillograms of the indicated parts of the songs of *Stenobothrus nigromaculatus* shown in Figs 31–36.

Song (Figs 45–53). The calling song is a single echeme lasting about 3–5 s and consisting of about 40–55 syllables repeated at the rate of about 12–13/s. The echeme begins quietly, usually reaching maximum intensity about halfway through its duration. Oscillographic analysis shows that there are gaps in each syllable. Previously published accounts of the calling song of this species have been based almost entirely on Faber (1953), who gave lower figures for both the duration of the echeme ('2 oder etwas mehr Sekunden') and the syllable repetition rate (8–9½/s), although suggesting that these figures applied to males singing in full sunshine. Faber's observations were made in the laboratory on males collected for him from Oberweiden, east of Vienna in Lower Austria, whereas mine were made in the field in southern France; in France I would expect such a low syllable repetition rate only in dull weather or at unusually low air temperatures.

In the presence of a female the male produces a long and complicated courtship song (Figs 47, 50, 53), which has been fully described by Faber (1953: Beilage 4).

Distribution. In western Europe this species seems to be confined to two isolated areas: southern France and central Spain. Further east it occurs from Austria eastwards across eastern Europe (including the Balkan Peninsula) and central Asia to Mongolia.

Stenobothrus festivus Bolívar

(Figs 2, 54–61)

Stenobothrus festivus Bolívar, 1887: 94. Syntypes of both sexes, Spain: Uclés, Aranjuez, San Ildefonso, Escorial, Gredos, Navacerrada (?MNCN, Madrid).

References to song. No published work known to me.

Recognition. This species is perhaps most likely to be confused with *grammicus* or *bolivarii*, which share with *festivus* the strongly inflexed pronotal lateral carinae. However, males of *festivus* lack the modified or characteristically coloured last palpal segments shown by the other two species, and in both sexes the pronotal lateral carinae are more sharply angled in the prozona, where they are clearly interrupted by an additional transverse sulcus on each side of the pronotum (Fig. 2).

In the field the single echeme of the male calling song enables this species to be distinguished easily from *grammicus* and *bolivarii*, which both produce a rapid sequence of echemes. The male calling songs of *fischeri* and *stigmaticus* are more similar, but *fischeri* has a longer echeme, with more than 40 syllables (usually fewer than 30 in *festivus*) and in *stigmaticus* the syllable repetition rate is usually more than 12/s (less than 12/s in *festivus*).

Song (Figs 54–61). The calling song is a single echeme lasting about 2–3 s and consisting of about 20–30 syllables repeated at the rate of about 7–11/s. The echeme usually begins quietly, reaching maximum intensity about halfway through its duration or a little earlier, but sometimes it begins more abruptly and sometimes there are one or more louder syllables before the quiet beginning. Oscillographic analysis shows that there is a characteristic pattern of gaps in the syllables: at the beginning of the echeme the syllables are completely broken up by gaps, but as the echeme progresses the gaps gradually disappear so that there are usually no gaps in the last few syllables. In a song produced by only one hind leg the gaps often persist until rather later in the echeme (Fig. 57), since there is no tendency for the gaps in the syllables produced by one hind leg to be obscured by sounds produced by the other.

Distribution. Widespread in the Iberian Peninsula and occurring locally in southern France.

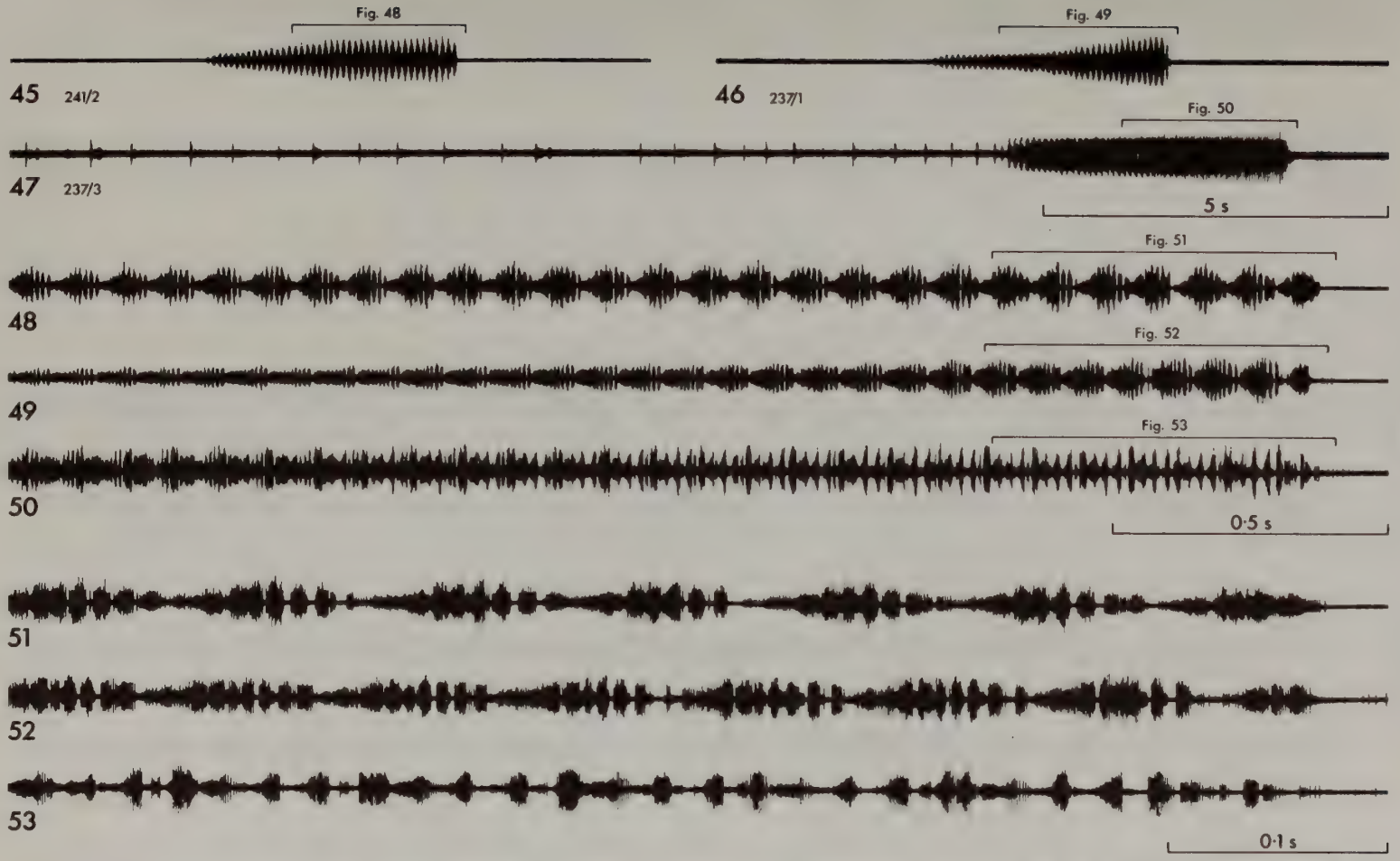
Stenobothrus grammicus Cazurro

(Figs 62–72)

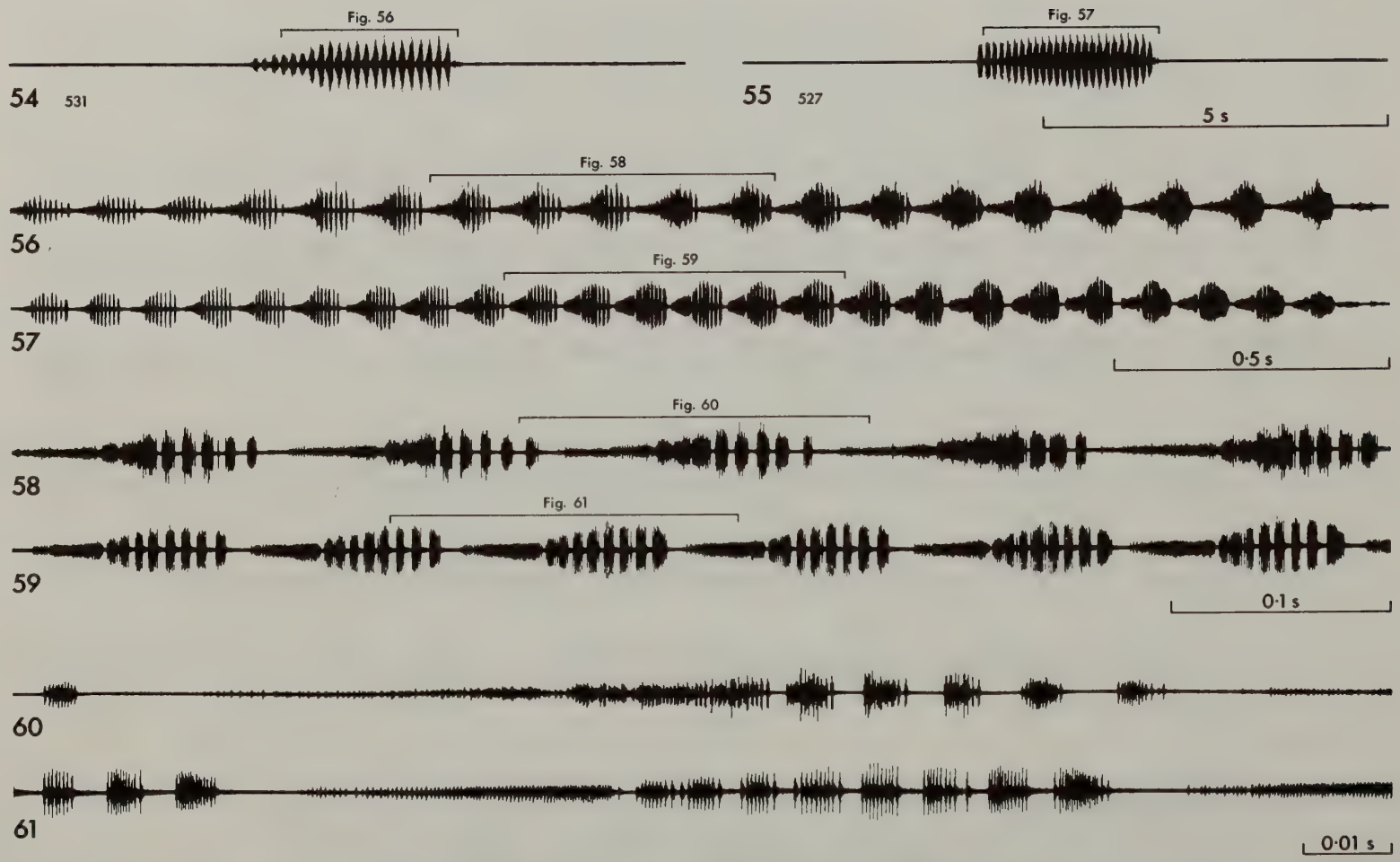
Stenobothrus grammicus Cazurro, 1888: 457. Syntypes of both sexes, Spain: Navacerrada, Peñalara, Escorial, San Ildefonso, Oña (?MNCN, Madrid).

References to song. **Diagram**: Luquet, 1978.

Recognition. Both sexes of this species may be recognized easily by the palps, which are black or dark



Figs 45–53 Oscillograms at three different speeds of the songs of three males of *Stenobothrus fischeri*. 45, 46, 48, 49, 51, 52. Calling songs. 47, 50, 53. Courtship song. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 395).



Figs 54–61 Oscillograms at four different speeds of the calling songs of two males of *Stenobothrus festivus*, one (54, 56, 58, 60) with two hind legs and the other (55, 57, 59, 61) with one hind leg. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 395, 396).

brown at the tip. In addition the male antennae are curved outwards and noticeably thickened and darkened towards the tip.

In the field the distinctive calling song, consisting of about 10–30 very brief and rapidly repeated echemes, enables males to be easily distinguished from most other species of *Stenobothrus*; however, oscillographic analysis is necessary to show clearly the difference from the calling song of *bolivarii*, which has longer echemes with a rather different syllable structure (see below).

SONG (Figs 62–72). The calling song consists of a sequence of about 10–30 echemes lasting about 5–15 s; the echemes are thus repeated at the rate of about 2/s. Each echeme lasts about 40–80 ms and is composed of a series of 4–8 syllables. The only other species of *Stenobothrus* known at present to have a rather similar calling song is *bolivarii*, but oscillographic analysis shows that species to have longer echemes, lasting about 80–110 ms, with a rather different syllable structure: in *grammicus* the loudest syllables are towards the end of each echeme, whereas in *bolivarii* the loudest syllable is at the beginning (cf. Figs 71, 76).

Luquet (1978: 427) gives the rather lower number of 6–8 echemes in each sequence of the calling song, based on observations in the Mont Ventoux area of Vaucluse in SE. France. My own studies of four males at two localities, also in the region of Mont Ventoux, suggest that this number is unusually low.

In the presence of a female the male produces a series of quieter and much longer echemes (Figs 64, 67, 70). Each of these echemes lasts for about 1–2 s and consists of a soft, continuous and rather amorphous sound. Between the echemes there are intervals of varying duration (usually between 3 and 15 s), during which quieter sounds are often produced.

DISTRIBUTION. Known only from upland areas in southern France and the Iberian Peninsula.

Stenobothrus bolivarii (Brunner)

(Figs 73–76)

Gomphocerus (Stenobothrus) bolivarii Brunner, *in* Bolívar, 1876: 327. LECTOTYPE: ♂, SPAIN: Sierra de Guadarrama, La Granja (NM, Vienna), here designated (see p. 399) [examined].

REFERENCES TO SONG. No published work known to me.

RECOGNITION. Males of this species may be recognized by the maxillary palps, in which the last segment is bulbous and usually coloured orange-pink or reddish brown. Females are more difficult to recognize, as the last segment of the maxillary palps is more normal in shape and is not always distinctively coloured like that of the male; however, in the upland areas of the Iberian Peninsula where *bolivarii* occurs the only other species of *Stenobothrus* with which females are likely to be confused is *grammicus*, in which both pairs of palps have black or dark brown tips in both sexes.

In the field the short, rapidly repeated echemes of the calling song enable males to be easily distinguished from most other species of *Stenobothrus*; the calling song of *grammicus* is, however, rather similar and oscillographic analysis is necessary to show clearly that *bolivarii* has longer echemes with a different syllable structure.

SONG (Figs 73–76). The calling song is quite similar to that of *grammicus*, consisting of a sequence of about 10–20 echemes lasting about 4–8 s; the echemes are repeated at the rate of about 2–3/s. Each echeme lasts about 80–150 ms and is composed of a series of about 5–10 syllables; the echemes are thus rather longer than those of *grammicus* and show a different syllable structure, with the loudest sound at the beginning of each echeme (cf. Figs 71, 76).

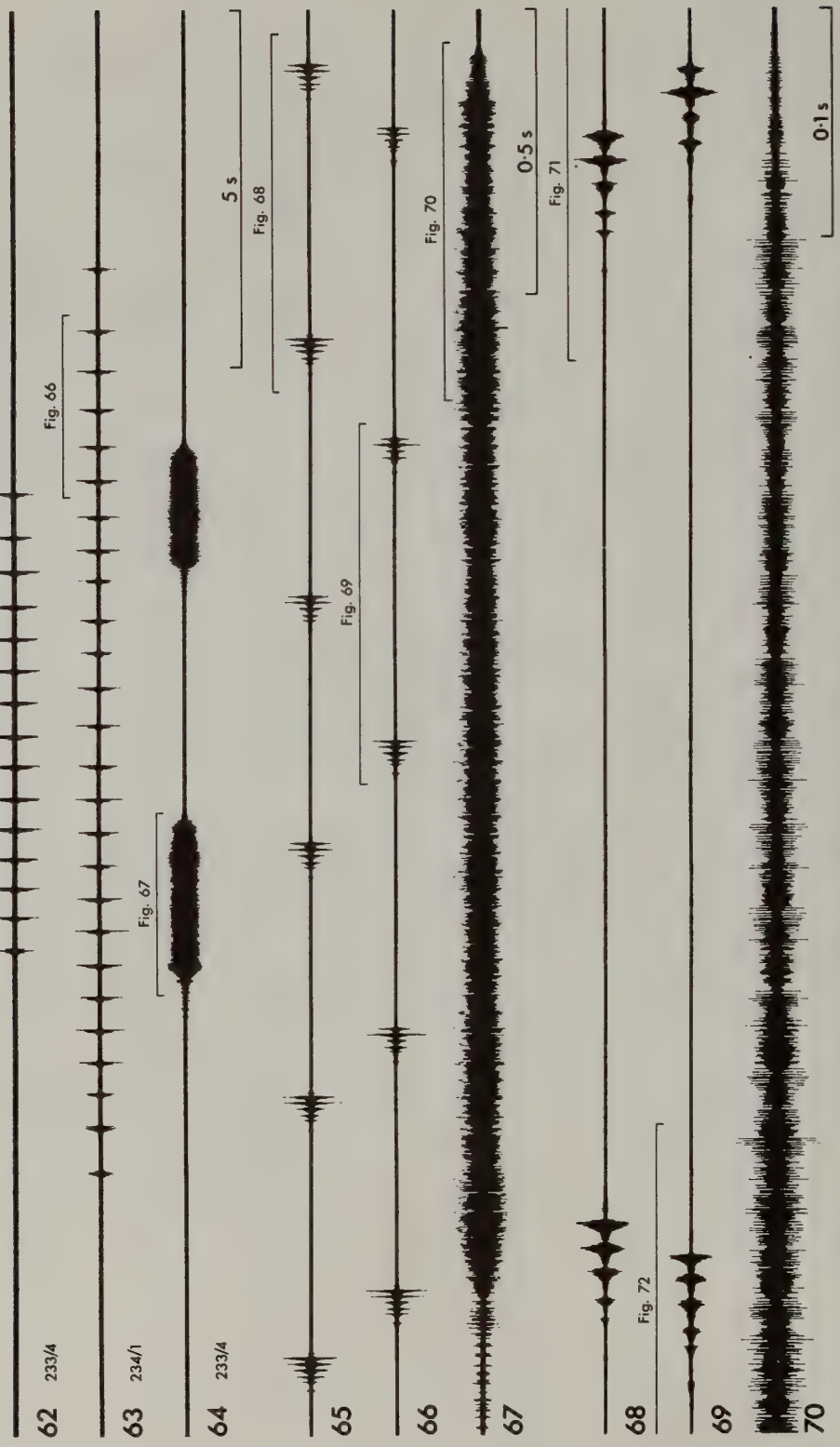
DISTRIBUTION. Known only from upland areas in the Iberian Peninsula.

Stenobothrus stigmaticus (Rambur)

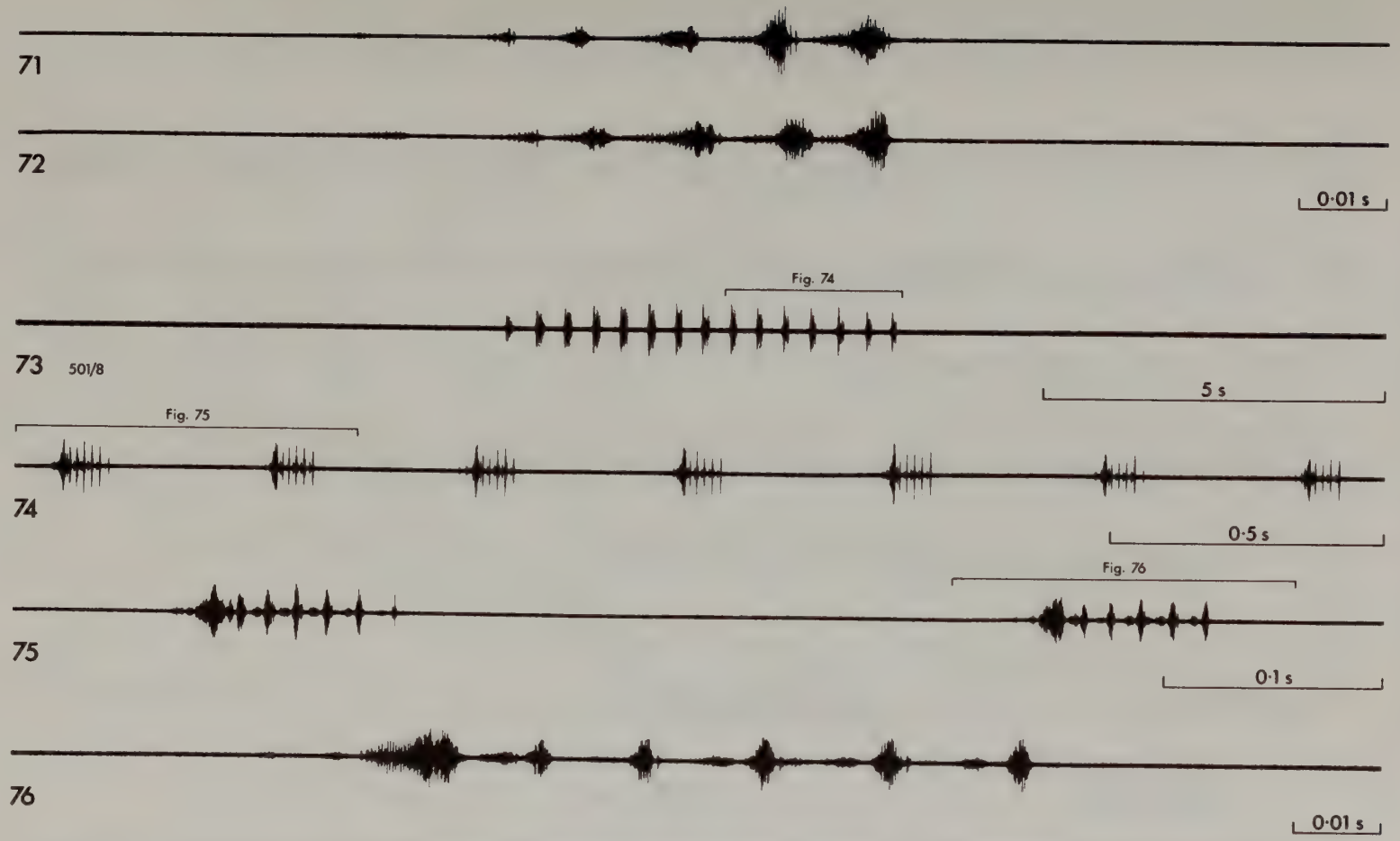
(Figs 7, 77–93)

Gryllus stigmaticus Rambur, [1838]: 93. Syntypes of both sexes, SPAIN: Sierra Nevada (lost); the two 'neotypes' designated by Harz (1975: 768) are clearly invalid.

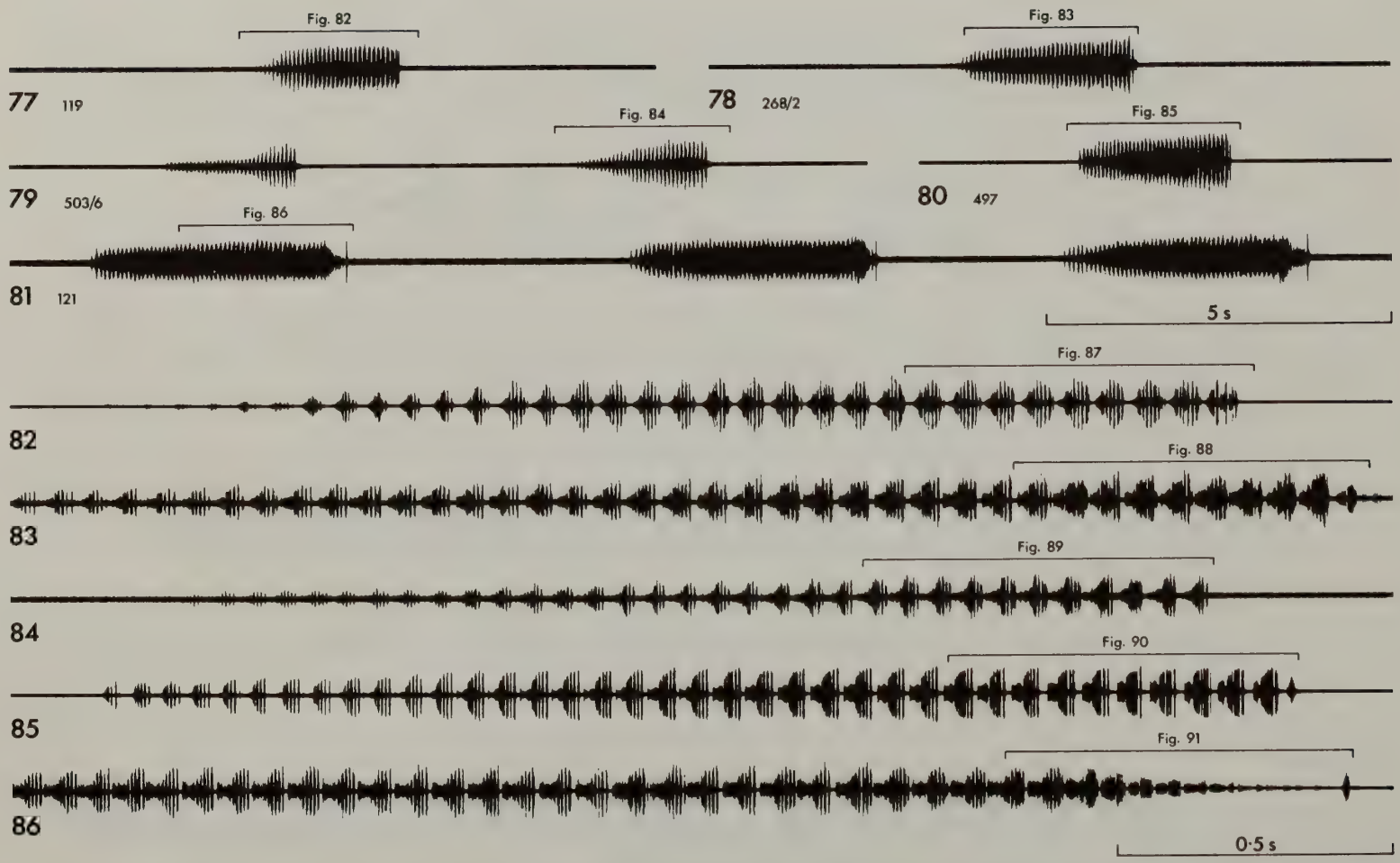
REFERENCES TO SONG. **Oscillogram**: Grein, 1984. **Diagram**: Bellmann, 1985*a*; Duijm & Kruseman, 1983;



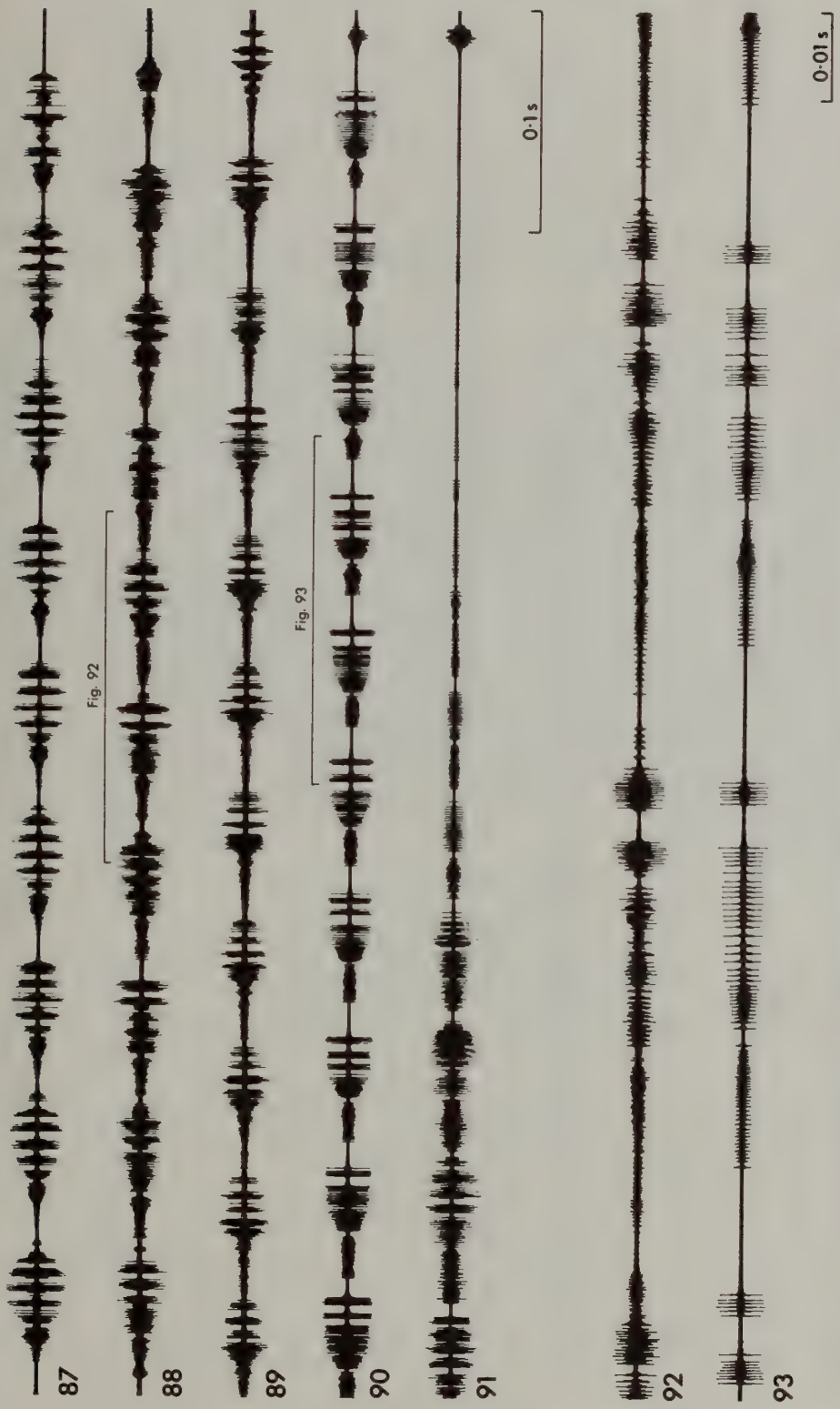
Figs 62–70 Oscillograms at three different speeds of the songs of two males of *Stenobothrus grammicus*. 62, 63, 65, 66, 68, 69. Calling songs. 64, 67, 70. Courtship song of the same male as Figs 62, 65, 68. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 395).



Figs 71–76 Oscillograms of the male calling songs of *Stenobothrus grammicus* and *bolivarii*. 71, 72. Faster oscillograms of the indicated parts of the songs of *S. grammicus* shown in Figs 68, 69. 73–76. Oscillograms at four different speeds of a male calling song of *S. bolivarii*. The number 501/8 refers to the recording from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 395).



Figs 77–86 Oscillograms of the songs of five males of *Stenobothrus stigmaticus*. 77–80. Calling songs of males with (77–79) two hind legs and (80) one hind leg. 81. Part of a courtship song. 82–86. Faster oscillograms of the indicated parts of the songs shown in Figs 77–81. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 395, 396).



Figs 87–93 Faster oscillograms of the indicated parts of the songs of *Stenobothrus stigmaticus* shown in Figs 77–86. Figs 90 and 93 are from a male with only one hind leg.

Jacobs, 1950, 1953; Ragge, 1965. **Verbal description only**: Broughton, 1972; Faber, 1928, 1953; Harz, 1957. **Disc recording**: Grein, 1984; Ragge, Burton & Wade, 1965. **Cassette recording**: Bellmann, 1985*b*.

Recognition. *S. stigmaticus* is conspicuously smaller than any other fully winged species of *Stenobothrus* occurring in western Europe. Were it not for the size difference it could be confused with *nigromaculatus*, but the veins Cu_1 and Cu_2 are much more widely separated in the fore wings than in that species.

In the field the male calling song, usually consisting of a single echeme lasting 1–3 s, enables this species to be distinguished easily from all other species of *Stenobothrus* with overlapping distributions except *fischeri* and *festivus*; these species produce single echemes of a similar kind to *stigmaticus*, but in *fischeri* the echeme is longer, with more than 40 syllables (fewer than 40 in *stigmaticus*), and in *festivus* the syllable repetition rate is less than 12/s (usually more than 12/s in *stigmaticus*). Both the calling and courtship songs are extremely similar to those of *apenninus*, but as that species is confined to the Apennines, where *stigmaticus* does not occur, confusion between the songs of these two species is unlikely. (See also the remarks on pp. 397, 399.)

Song (Figs 77–93). The calling song is a rather quiet echeme lasting about 1–3 s and consisting of about 25–40 syllables repeated at the rate of about 10–20/s (usually 14–18/s). The echeme usually begins quietly, reaching maximum intensity within about one second. Oscillographic analysis shows that there are usually gaps in the syllables, especially near the beginning of the echeme, but they are not always very clear. The echemes are usually produced singly and repeated at irregular intervals, but occasionally two echemes are produced within a few seconds of each other (Fig. 79).

In the presence of a female the male produces a series of echemes separated by intervals of about 2–7 s (Figs 81, 86, 91). Each echeme is similar to that of the calling song, but is quieter, longer (usually lasting 3–5 s and composed of about 50–70 syllables) and with one hind leg moving more vigorously than the other; the last few syllables are rather modified and then the hind leg that has been moving more vigorously produces a short, loud syllable by a very quick downstroke. The more vigorously moving hind leg alternates from one side to the other in successive echemes. Sometimes the loud syllable at the end of each echeme is omitted.

Distribution. Widespread in western and central Europe, but not reaching as far north as Scandinavia. In southern Europe it occurs in the mountainous parts of the Iberian Peninsula and the northern part of the Balkan Peninsula but is apparently absent from the Italian Peninsula (although occurring in the Italian Alps). It is recorded from the Rif mountains in Morocco and its range extends eastwards into European Russia and Asia Minor.

Stenobothrus apenninus Ebner
(Figs 94–102)

Stenobothrus apenninus Ebner, 1915: 551. LECTOTYPE ♂, Italy: Lazio, Monti Reatini, Terminillo, 6.viii.1912 (*R. Ebner*) (NM, Vienna), here designated (see p. 399) [examined].

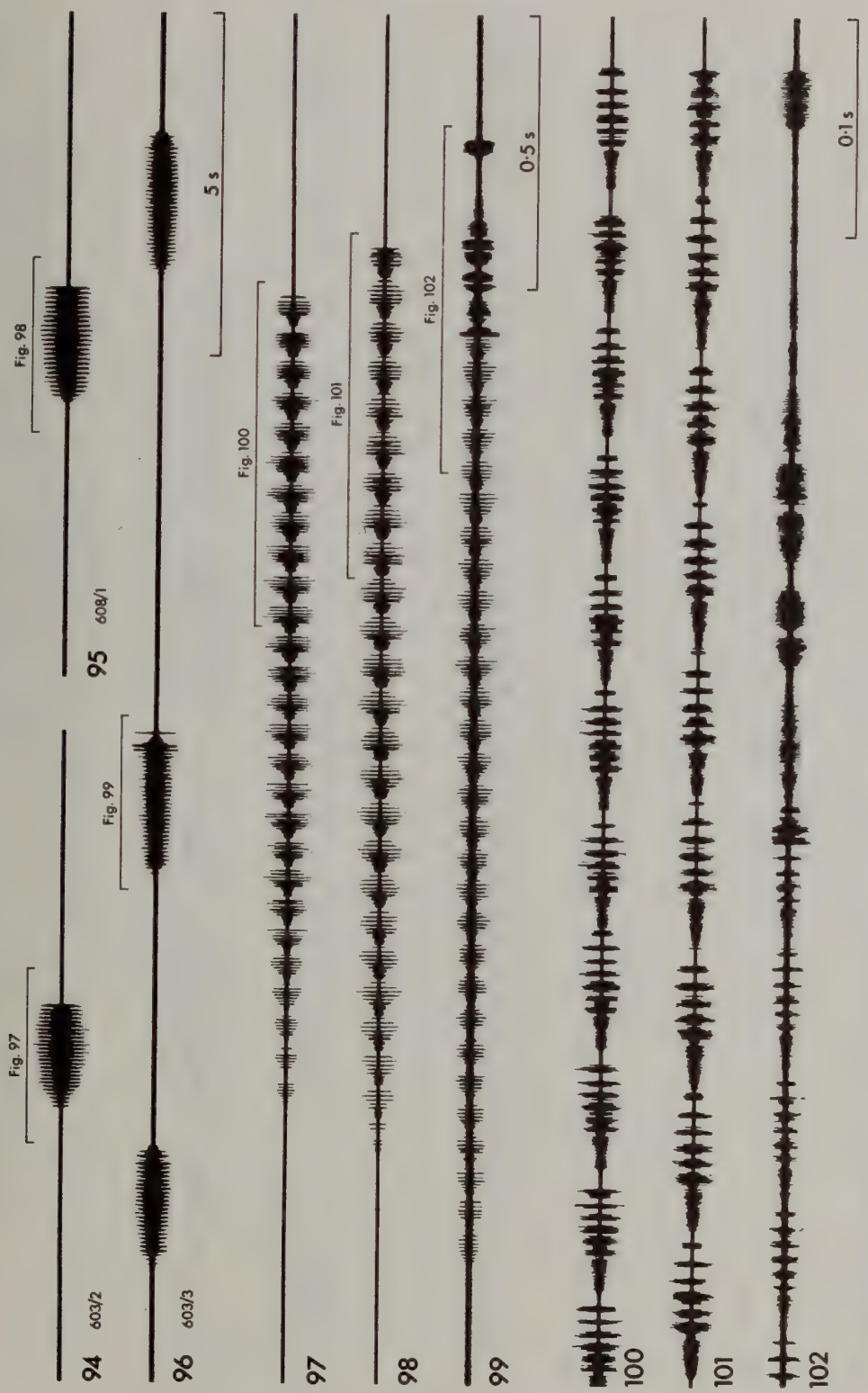
References to song. The only published reference to the song known to me is that of Harz (1975: 770), in which he quotes Faber as having told him in 1971 that the song was indistinguishable from that of *stigmaticus*.

Recognition. This montane species is endemic to the Apennine range in the Italian Peninsula, where it may be easily distinguished from other species of *Stenobothrus* by the vestigial hind wings of both sexes and the much reduced fore wings of the female. In the field the calling song of the males, consisting of a single echeme lasting 1–2 s, also enables this species to be distinguished easily from Italian species of the genus occurring in the Apennines.

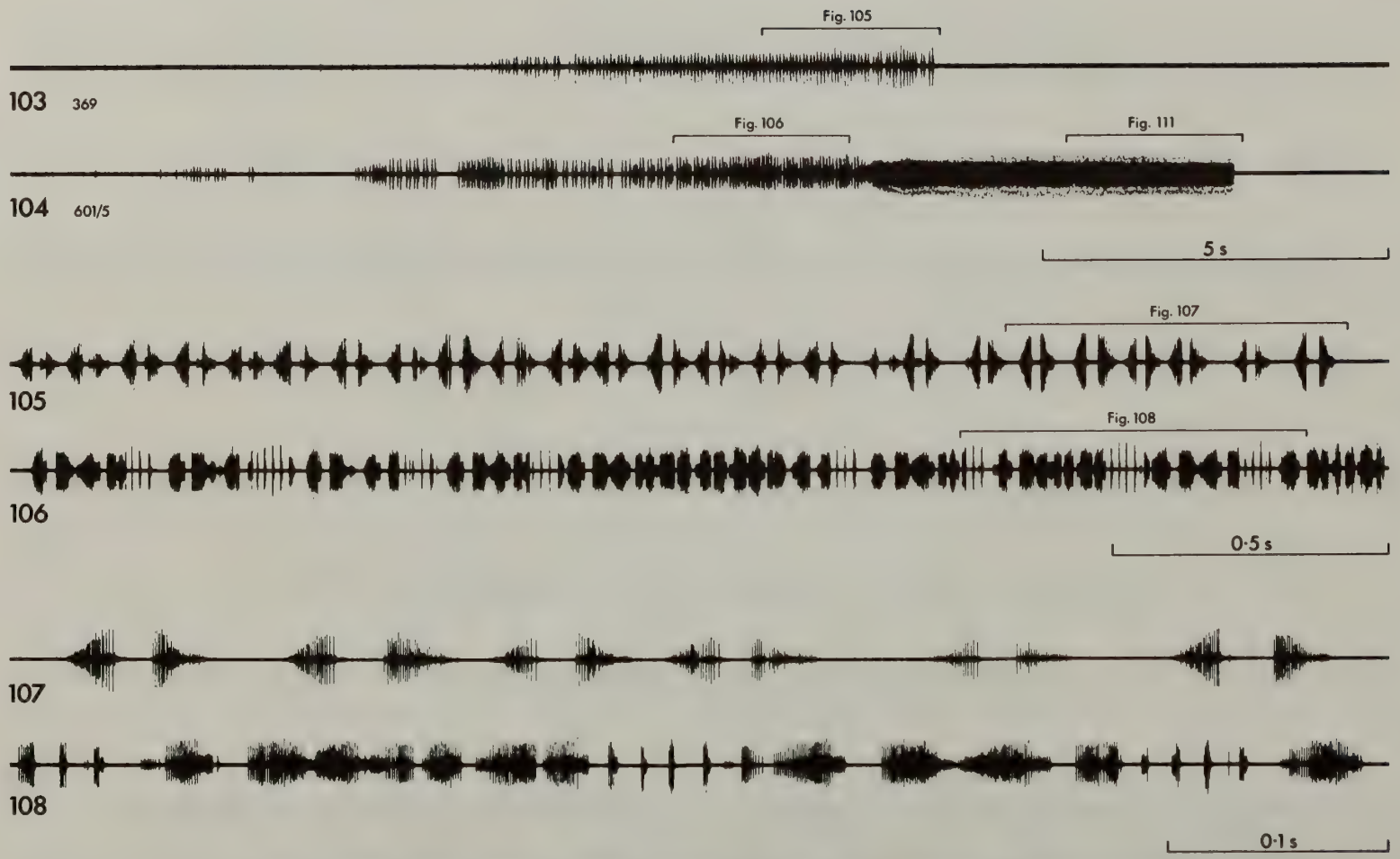
Song (Figs 94–102). The calling song is a single echeme lasting about 1–2 s and consisting of about 20–30 syllables repeated at the rate of about 15–20/s. The echeme usually begins quietly but reaches maximum intensity within 0·5 s. Oscillographic analysis shows that there are clear gaps in the syllables throughout the echeme.

In the presence of a female the male produces a quieter courtship song (Figs 96, 99, 102) very similar to that of *stigmaticus* (see above) but with shorter echemes (often lasting about 2 s and composed of about 30 syllables).

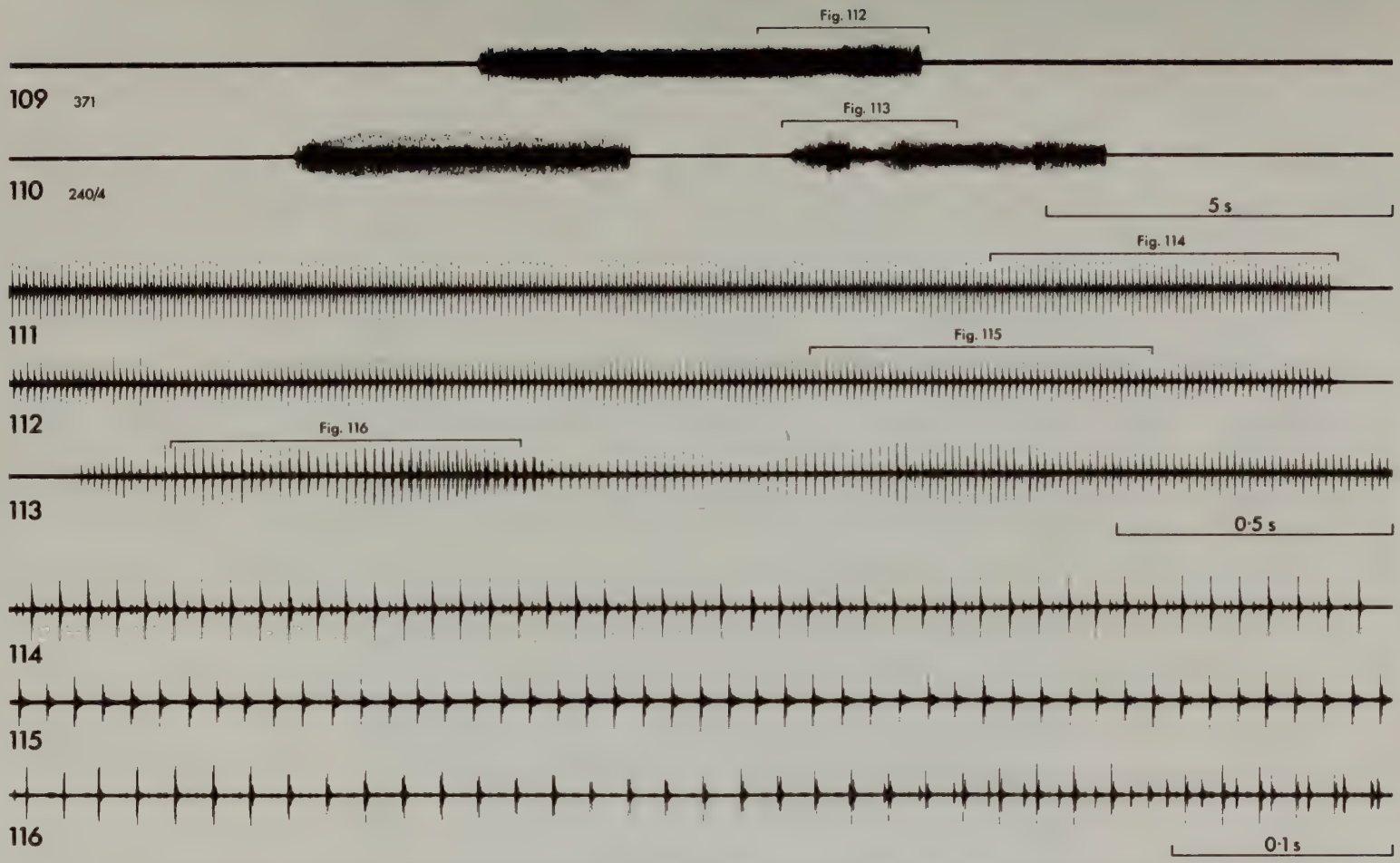
Distribution. Known only from the Apennine range in Italy.



Figs 94–102 Oscillograms at three different speeds of the songs of three males of *Stenobothrus apenninus*. 94, 95, 97, 98, 100, 101. Calling songs. 96, 99, 102. Courtship song. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 396).



Figs 103–108 Oscillograms at three different speeds of the calling songs and wing-buzz of two males of *Stenobothrus rubicundulus*. 103. An echeme of purely femoro-alary stridulation. 104. A femoro-alary echeme followed immediately by a wing-buzz while the male remained on the ground. 105–108. Faster oscillograms of the indicated parts of the femoro-alary stridulation shown in Figs 103 and 104. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (p. 396).



Figs 109–116 Oscillograms of the wing-buzzes of three males of *Stenobothrus rubicundulus*. The wing-buzz shown in Fig. 109 and the first wing-buzz shown in Fig. 110 were produced while the male was on the ground, but part of the second wing-buzz shown in Fig. 110 was produced during hovering flight. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (p. 396).

Stenobothrus rubicundulus Kruseman & Jeekel

(Figs 8, 103–116)

Gryllus miniatus Charpentier, 1825: 155. Syntypes of both sexes, AUSTRIA: Alps, and GERMANY: 'in Saxoniae montibus' (lost); the two 'neotypes' designated by Harz (1975: 775) are clearly invalid. [Primary homonym of *Gryllus miniatus* Pallas, 1771: 467.]

['*Stenobothrus rubicundus* (Germar)'; Yakobson & Bianki, 1902: 223, and other authors. Misinterpretation of Germar (1817: 256) and misidentification of *Gryllus (Locusta) rubicundus* Goeze, 1778: 108.]

Stenobothrus rubicundulus Kruseman & Jeekel, 1967: 79. [Replacement name for *Gryllus miniatus* Charpentier.]

REFERENCES TO SONG. **Oscillogram**: Elsner, 1974*b*. **Verbal description only**: Chopard, 1952; Faber, 1953; Harz, 1957.

RECOGNITION. The very broad fore wings, with unbranched *M*, regular ladder-like cross-veins in the medial area, and Cu_1 and Cu_2 quite clearly separated (Fig. 8), enable males of this species to be recognized quite easily. In the female these characters of the fore wing are not so clearly developed, but the hind wings of both sexes have an unbranched *M* and greatly enlarged medial area, and the more distal part of the anterior margin is heavily sclerotized and conspicuously dark in colour (Fig. 8).

In the field males may be easily recognized by their highly characteristic calling song, which includes a loud buzzing sound produced by wing-vibration, either on the ground or in hovering flight.

SONG (Figs 103–116). The calling song is composed of two quite different kinds of sound: one is produced by the usual femoro-alary stridulation and the other by wing-vibration, either on the ground or in flight. The song sometimes consists of femoro-alary stridulation immediately followed by wing-vibration, but each kind of sound production may occur without the other.

The femoro-alary stridulation (Figs 103–108) usually begins with a series of syllables in which the upstroke and downstroke of the hind legs produce clearly separated, simple sounds (Figs 105, 107); the syllable repetition rate is variable, but is usually 8–13/s. After a few seconds the pattern is often complicated by some of the downstrokes being prolonged and broken up by gaps (Figs 106, 108). This femoro-alary echeme usually lasts for about 6–10 s, after which it may be followed immediately by wing-vibration (Fig. 104).

The wing-vibration produces a loud buzzing sound (Figs 109–116) usually lasting about 4–10 s. According to Elsner (1974*b*) the sound is produced by the strongly sclerotized anterior margins of the two hind wings being beaten against each other. Oscillographic analysis shows the buzzing to consists of a series of sharply distinct short-lived sounds repeated at the rate of about 55–85/s (Figs 111–116). The whole of the wing-buzz may be produced while the male is sitting on the ground, but often the male takes off and continues to produce the buzzing sound in flight, often hovering above the ground (Fig. 110, second wing-buzz).

In the presence of a female the male begins with femoro-alary syllables similar in kind to those of the calling song, but the echeme is often greatly prolonged, sometimes lasting for more than 30 minutes. This is followed by wing-vibration and there is then often an alternation of shorter echemes of femoro-alary stridulation and bursts of wing-vibration. A sequence of this kind may end in the male taking off during a burst of wing-vibration and finally an attempt to copulate with the female.

DISTRIBUTION. This montane species is known only from the Alps, higher Apennines and mountains of the Balkan Peninsula.

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P. R. Ackery & R. I. Vane-Wright

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